On biological evolution and environmental solutions

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Abstract

Drawing insights from multiple disciplines is essential for finding integrative solutions that are required to tackle complex environmental problems. Human activities are causing unprecedented influence on global ecosystems, culminating in the loss of species and fundamental changes in the selective environments of organisms across the tree of life. Our collective understanding about biological evolution can help identify and mitigate many of the environmental problems in the Anthropocene. To this end, we propose a stronger integration of environmental sciences with evolutionary biology.

Keywords: Biological evolution, environmental science, biofuels, pollution, disease, harmful algal blooms

1.0 Introduction

All ecosystems, be they natural or engineered, contain biological organisms that are bound by the principles of biological evolution. As such, biological evolution is often a central feature of many problems that are currently being tackled by environmental scientists. Yet fundamental principles from the discipline of evolutionary biology are rarely used in the analysis and mitigation of environmental problems, even when evolutionary processes are closely linked to their manifestation (Carroll et al., 2014; Jørgensen et al., 2019). Environmental scientists are particularly adept at reaching across disciplines to ensure that they have the knowledge and tools necessary to tackle complex environmental problems. Here we propose that a wider application of principles of evolutionary biology would help us achieve more sustainable solutions to environmental problems.

In brief, evolution is a process of heritable change in the phenotype of a population of organisms (Box 1). While evolution can result from random genetic drift (representing “neutral” evolution), here we focus on adaptive evolution, defined as a change in population mean fitness in response to natural selection (Box 1). Genetic and trait variation, and how such variation changes over time and space, are fundamental properties of living systems. There is mounting evidence that evolution is sufficiently fast in natural populations to be highly relevant for understanding how populations will respond to human-mediated environmental change (Hendry, 2017; Hendry & Kinnison, 1999).

Applying evolutionary principles to understand environmental problems is not a novel idea (Gunderson and Holling 2002, Santamaria and Mendez 2012), but widespread application is still limited (Jørgensen et al., 2019). In the context of the biodiversity crisis ecologists are increasingly using evolutionary theory to help mitigate the loss of genetic and species diversity due to climate change and environmental pollution (Bell & Gonzalez, 2009; Kristensen et al., 2018). Evolutionary theory is also critical to understanding the emergence of antibiotic resistance in microbes (Palmer & Kishony, 2013) and chemical resistance in pests (Fisher et al., 2018). Plainly, evolutionary theory can be highly relevant to pertinent environmental problems, but it is not broadly applied. There is a frequent use of methods and technologies originating from evolutionary biology. In particular, molecular genetic methods are often used to characterise microbial community composition (Das & Dash, 2019), and the patterns of gene expression of individual organisms and communities (Oziolor et al., 2017). While such methods are undeniably useful to gain functional insights, they are rarely used in environmental science to study evolutionary *processes*. The potential for evolutionary applications in environmental sciences is far reaching, and in the next sections we focus on core concepts of evolution and exemplify how they can be applied to a range of environmental problems in aquatic ecosystems.

1.1 The structure of evolutionary processes

The structure and rate of change of heritable trait variation in living systems are particularly relevant for understanding environmental problems. Living systems are hierarchically structured, where the traits of individuals arise from the interpretation of the environment by genes (so called genotype-phenotype maps; (Houle et al., 2010)). Individuals interact within populations, where average trait values change through evolutionary and environmental processes (Burns, 1992; Frank, 2011; Pedersen & Tuomi, 1995), and populations interact and evolve within multi-species communities (Weber et al., 2017). As a result of this hierarchical structure, human activities affecting one level of biological organization can have unanticipated outcomes at another level (Gunderson and Holling 2002, Melián et al., 2018). For example, human activities that affect gene flow among populations can lead to the introduction of either beneficial alleles that help populations adapt to changing environments, or deleterious alleles that contribute to maladaptation of natural populations and thereby can potentially hinder conservation efforts (Leitwein et al., 2019). Despite the long held view that evolution is a slow process, it is now well established that the pace of heritable trait change can be sufficiently fast to affect population dynamics, species interactions, and ecosystem processes - i.e. evolution can act at ecological time scales (Hairston et al., 2005; Stockwell et al., 2003). The dynamics of species interactions in natural communities are hence not simply a product of past evolution. Rather, evolutionary processes can shape trait distributions of populations (i.e. mean and variance) at a pace that is highly relevant for many environmental problems.

Evolutionary processes can either ameliorate or exacerbate environmental problems. Evolutionary adaptation, for example, can drive the recovery of populations, or even multi-species communities, from decline, in a process known as “evolutionary rescue” (Bell & Gonzalez, 2009; Low-Décarie et al., 2015). In natural populations, evolution has rescued killifish from chemical pollution (Whitehead et al. 2017) and amphibians from acidification (Hangartner et al. 2012). In these cases, genetic adaptation has allowed for the persistence of populations in environments that would otherwise be unsuitable. Evolutionary novelty can also emerge in populations exposed to synthetic environments created by humans, and, in doing so, perform essential evosystem services (Rudman et al., 2017). For example, the artificial sweetener acesulfame (ACE) is a persistent compound in aquatic environments because it is resistant to microbial-mediated biodegradation both in natural and wastewater treatment environments (Kahl et al., 2018). Recent work suggests that the catabolism of this compound has evolved repeatedly in multiple wastewater treatment plants in Germany (Kahl et al., 2018), possibly associated with a microbial consortium of proteobacterial species (Figure 1). Identifying the evolutionary processes governing such bioremediation dynamics could help address the persistence of chemicals in our natural environments for which engineering solutions are lacking. On the other hand, evolutionary processes can also create novel environmental problems, or worsen existing ones. For example, the emergence and amplification of antibiotic resistance genes is a global problem, caused by the widespread overuse of antibiotics (Palmer & Kishony, 2013). In wastewater treatment plants, the concentration of antibiotic resistance genes may be amplified by evolution prior to water discharge into natural aquatic environments (Ju et al. 2018)

(Figure 1). Understanding and monitoring the evolutionary process in wastewater treatment plants could improve our ability to limit the release of antibiotic resistance genes into natural environments (Czekalski et al. 2015).

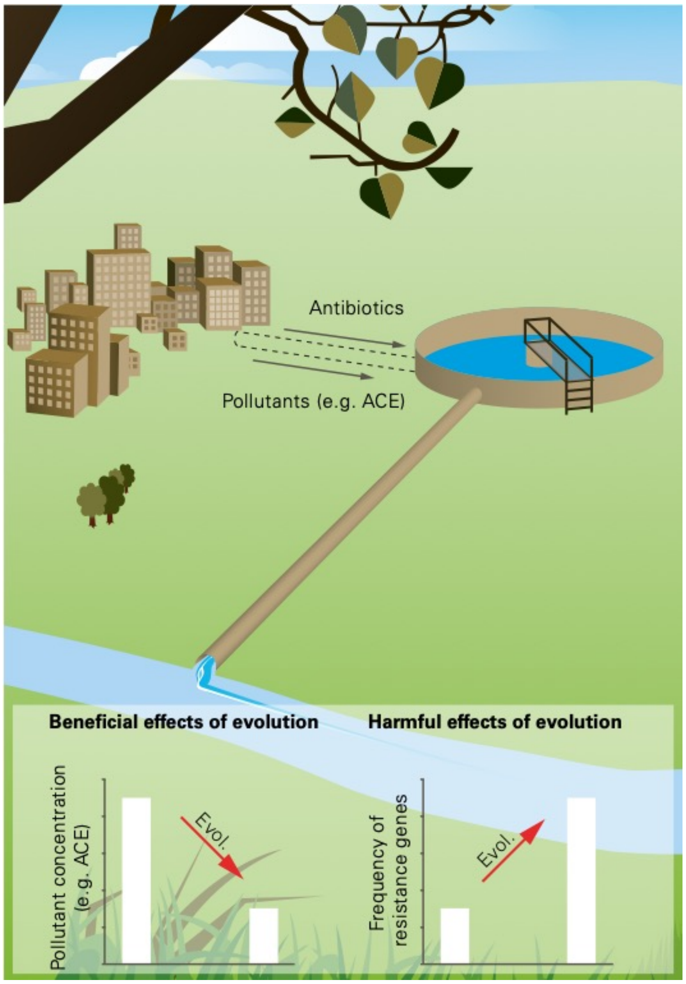

Figure 1: Two scenarios illustrating how microbial evolution within a wastewater treatment plant (WWTP) can either cause a beneficial reduction in a pollutant concentration (ACE: the artificial sweetener Acesulfame) due to the evolution of catabolism of novel/synthetic compounds, or an unwanted increase in resistance genes in a microbial population due to positive selection in the treatment plant (Figure design by Peter Penicka, Eawag).

2.0 Case studies

In this section, we illustrate how a broader application of evolutionary theory can enable environmental scientists to craft better solutions for environmental problems. To this end, we use four examples from aquatic systems: (i) emergence and epidemiology of disease, (ii) renewable production of biofuels, (iii) chemical pollution, and (iv) outbreaks of algal blooms.

2.1 Disease dynamics in natural populations: When evolution kills or cures

Diseases are among the most severe environmental problems. They are a threat to biodiversity (Fisher et al., 2018; Lips et al., 2006), to food production (Strange & Scott, 2005) and to human health (Jones et al., 2008). Disease outbreaks are often caused by pathogens that have undergone a recent host shift or expansion of their geographic range (Engering et al. 2013; Longdon et al. 2014). Most disease-causing organisms have large populations and short generation times, which generally facilitates rapid evolution. Consequently, disease emergence typically involves rapid co-evolutionary dynamics that stem from natural selection on both pathogen infectivity and host defence (Penczykowski et al. 2016). Rapid evolutionary dynamics are expected to take place at the onset of disease emergence, governed by the pathogens' and the hosts' evolutionary history.

Disease emergence is often a consequence of human activities. Transport between continents can bring pathogens into naïve host populations that are, at least initially, defenseless; they can lack sufficient genetic variation for resistance because they do not have coevolutionary history with these pathogens. The crayfish plague provides a good example. *Aphanomyces astaci*, a pathogen of freshwater crayfish native to North America came to Europe with introduced American crayfish (Svoboda et al., 2017). American crayfish species had evolved a high tolerance of the pathogen, due to their long evolutionary history, but the pathogen proved devastating to stocks of European freshwater crayfish species (Holdich et al., 2009). Likewise, human activities that modify ecosystems for food production can promote the emergence of locally highly virulent pathogens (Stukenbrock & McDonald, 2008). For example, large monocultures of genetically homogenous plants can facilitate the evolution of host specialization (McDonald and Stukenbrock 2016), leading to evolutionary dynamics that are not commonly observed in natural ecosystems.

Evolutionary theory can be instrumental in helping to understand the origin and spread of diseases through populations. Increasingly, researchers can track disease dynamics over time by comparing genetic variation among isolates, and such data can help inform policy decision and management of viral diseases, such as COVID-19 (Andersen 2020, Brussow 2020) and Ebola (Mbala-Kingebeni et al. 2019). Drug treatment is often the default approach used to control emergent bacterial and fungal diseases, but in some cases a single new drug can cause strong natural selection, and, combined with the high evolutionary potential of pathogens, this means that the expected time until drug resistance evolves can be short (Fisher et al., 2018; Kennedy & Read, 2018). For such scenarios, we need to develop evolution-aware strategies to avoid and control emergent diseases. For example, in the case of chemical treatments, combination therapy or the sequential application of different drugs can delay resistance evolution (Palmer & Kishony, 2013; Roemhild et al., 2018), and the development of ‘evolution-proof’ drugs is a particularly attractive idea (Bell & MacLean, 2018). Alternative strategies include fighting the disease with agents that are able to evolve themselves, such as microbial symbionts that provide protection against the disease (Kueneman et al., 2016).

2.2 Renewable biofuels: When evolution fills our tanks

The dwindling supply and the negative environmental impact of fossil fuels have spurred substantial research and investment into using biofuels as a renewable and sustainable source of energy (Sheehan et al., 1998). Among the many potential sources of biomass for biofuels, phytoplankton or “algal” biofuels are among the most efficient in terms of land-use and energy production per unit biomass (Y. Chisti, 2008; Yusuf Chisti, 2007). Until now, algal biomass production for biofuel has heavily focused on the production of single species with desirable properties, namely high lipid content, fast growth rates, and resistance to disease and grazers. However, farming monocultures is notoriously difficult because individual species or strains, be they algae or crops, can never possess all of the desirable traits for long-term stable crop production at high yields (Smith et al., 2010). The ideal species for maximum production would be unconstrained by the trade-offs inherent to all living systems. Yet such omnipotent organisms, known in evolutionary biology as Darwinian demons (Krakauer, 2011; Law, 1979), do not exist and cannot be engineered. Nevertheless, sustainable yield of biofuels could be optimized by understanding the biochemical and biophysical basis of the fundamental trade-offs between growth rate, lipid production and traits that make better competitors, confer resistance to parasites, and are resistant to grazers (Shurin et al., 2013, 2016; T. Yoshida et al., 2004). Understanding the evolution of ecologically relevant traits, under different biotic and abiotic contexts, may improve the stability and efficiency of biofuel production.

The application of evolutionary theory to algal biofuel production is in its infancy, but holds immense potential. Algal populations are large and have short generation times. Usually the populations maintain high phenotypic and genetic diversity (Brandenburg et al., 2018; Chen & Rynearson, 2016; Lebret et al., 2012; Masseret et al., 2009; Rynearson & Armbrust, 2000). Evolution in such populations can be fast if selection is strong (Thibodeau et al., 2015; Takehito Yoshida et al., 2003). Harnessing the adaptive evolutionary potential of algal populations could help us explore the range of feasible trait space to obtain desirable trait combinations. For example, researchers are currently trying to simultaneously improve the yield of triacylglycerols in culture (used to produce fatty acid methyl esters needed used in biodiesel production), while concurrently maximizing population growth rates, trait combinations which are normally mutually exclusive. Approaches include genetic engineering (Zeng et al., 2011), directed evolution via successive rounds of mutagenesis and selection (Johnson et al., 2016; Lewin et al., 2016), and selection on the existing levels of genetic variation in a population (Mooij et al., 2013; Shurin et al., 2016).

While evolution might help us improve biofuel production (Kazamia et al., 2014), it might also culminate in undesirable outcomes. For example, engineering solutions imagined based on evolutionary trade-offs might be eroded over time due to mutation, horizontal gene transfer, and recombination. Custom designed biofuel production systems should consider the evolutionary consequences of rapid harvesting. For example, rare beneficial mutations arising during population expansion, might be periodically lost before they sweep to dominance in the populations (Bull & Collins, 2012; Shurin et al., 2016). In short, evolution offers both promises and pitfalls for biofuel production.

2.3 Chemical Pollutants: When evolution is, and is not, the solution to pollution

Chemical pollution is a global problem with a local character (Grimm et al., 2008; Halpern et al., 2008; Vörösmarty et al., 2010). Chemical pollution often stems from chemical pest control applied in agricultural production, as well as from the unwanted waste produced by human population growth and industrial activities. Wastewater treatment plants can only remove and target compounds that pass through the sewage system; many other compounds still enter the natural environment in a diffuse manner, especially from agriculture. These chemical compounds can have toxic effects on individual organisms and these effects can be enhanced when they occur in mixtures (Abdelghani et al., 1997; Connon et al., 2012). For instance, pest control requires highly biologically active substances to target unwanted algae, fungi and arthropods. When pesticides then leak into ecosystems that are not the target of the application, this can change food web structure and influence ecosystem function (Stamm et al., 2016).

Because pollution and the ecological context in which pollution occurs are often highly local, we can expect pollution to have many different evolutionary consequences in natural ecosystems. However, the biological effects of pollutants are typically studied using a limited number of model species and strains, usually in oversimplified ecological contexts that might underestimate their effects in nature (Relyea & Hoverman, 2006). Furthermore, many of the approaches used in environmental science and ecotoxicology to assess the environmental effects of pollutants only test a few selected genetic lineages of organisms (e.g., single strains of *Daphnia*), and often ignore both within-population variation in sensitivity to pollutants and the effects of mixtures of pollutants on organisms. For example, morphologically similar but genetically distinct lineages of amphipods, within the *Gammarus fossarum* cryptic species complex, vary in their sensitivity to the fungicide tebuconazole and the insecticide thiacloprid (Feckler et al., 2012). Such lineage diversity within species is rarely accounted for in typical assessments of pollutants on organisms (Relyea & Hoverman, 2006). Synthetic chemicals present a particular challenge because the exposed organisms may lack the exposure history necessary for the emergence of an evolutionary adaptation. Synthetic chemicals can also act as mutagens that disrupt the homeostasis of organisms (Bickham et al., 2000).

Chemical toxicity can rapidly drive populations to such small sizes that their persistence over time becomes threatened (Williams & Oleksiak, 2008). Interestingly many classic studies about rapid evolution involve chemical pollution, such as the evolution of resistance to pesticides, resistance to antibiotics or mining-related metal pollution (Hoffmann & Parsons, 1997; Palumbi, 2009) and, more recently, pollutant induced elevated mutation rates and rapid adaptation (Brady et al., 2017; Coutellec & Barata, 2013; Kimberly & Salice, 2012; Loria et al., 2019; Palumbi, 2009). Evolutionary adaptation to chemical pollution can also rescue populations from extinction caused by demographic decline. For example, experimental *Daphnia* populations that were initially highly sensitive to metal contamination recovered rapidly via genetic adaptation (Hochmuth et al., 2015). In another example, natural killifish populations inhabiting urban estuaries adapted to lethal levels of pollutants with genetic adaptations (Oziolor et al., 2017; Reid et al., 2016). Unsurprisingly, adaptation of a population can also be an unwanted outcome of management, such as when the evolution of resistance reduces the sensitivity of a species used in ecological risk assessment (Morgan et al., 2007). Evolution's ability to alter the direction of responses to environmental change, such as that brought by chemical pollution, is one of the main arguments for including evolutionary concepts in environmental research. Finally, potential for evolutionarily based solutions to pollution comes from implementing bioremediation, such as designing microbial communities that have evolved the ability of biodegradation of chemicals (Liu & Suflita, 1993).

2.4 Algal blooms: When evolution muddies the waters

Harmful algal blooms are often associated with eutrophication, pollution and climate change (Huisman et al., 2018; Monchamp et al., 2018). Harmful algal blooms, which can persist for weeks or months, may foul drinking water, turn lakes anoxic and kill fish, and render lakes unacceptable for recreational use (Lewitus et al., 2012; Paerl et al., 2011). Ecological theory suggests that blooms develop when nutrient input releases phytoplankton from control by grazers (Abrams & Walters, 1996; Gragnani et al., 1999; Pančić & Kiørboe, 2018). Additionally, evolutionary processes are also relevant to the emergence, volume and toxicity of blooms. Indeed, we postulate that trying to manage harmful blooms without Darwin, is like trying to fly to the moon without Newton (modifying Andrew Read's concluding remark on his TEDMED talk on importance of evolutionary medicine: https://www.tedmed.com/talks/show?id=7286).

The trade-off between resource uptake and grazing resistance is at the root of the ecological and evolutionary causes of bloom biomass (Cloern, 2018). Selective grazing by zooplankton will deplete edible algae and, subsequently, increase the abundance of well-defended algae (Hairston et al., 2005; Takehito Yoshida et al., 2003). Harmful algal blooms are characterised by an array of defense traits that are favored by natural selection. Some algae produce compounds that are toxic to grazers, such as the neurotoxins, saxitoxins and domoic acid produced by dinoflagellates, cyanobacteria, and diatoms, respectively (Pančić & Kiørboe, 2018; Xu & Kiørboe, 2018). Remarkably, toxin production varies widely both within and among populations. For example, some lineages entirely lack the genes for toxin production (Brandenburg et al., 2018; Briand et al., 2009). The evolutionary dynamics of different toxic/non-toxic genotypes during algal blooms is likely driven by physiological trade-offs between costs of toxin production and resource uptake for growth (Brandenburg et al., 2018; Cadier et al., 2019; Chakraborty et al., 2019; Kiørboe & Andersen, 2019). Such defense-growth trade-offs are likely important for the emergence of harmful algal blooms (Burford et al., 2019; Jankowiak et al., 2019; Kim et al., 2010; Li et al., 2012), but the selective factors that favour toxic variants in bloom forming algae are not fully understood. Identifying the evolutionary processes involved in algal blooms would likely help us predict which algal blooms might turn toxic. In a first step, reliable prediction would enable the avoidance of risks associated with toxic algal blooms (e.g. by timely establishment of exclusion zones), and in a second step, it could inform mitigation measures to reduce the occurrence of algal blooms (e.g. by influencing relevant selective forces such as nutrient input).

3.0 Evolving the environmental sciences

Evolutionary processes are often an inescapable and critical component of both understanding and solving environmental problems. The evolution of resistance genes will continually challenge our efforts to halt diseases through the development of new drugs, highlighting the need to complement efforts in drug discovery with the development of evolution-aware application strategies. A better appreciation of evolution’s limits and, in particular, the impossibility of Darwinian demons, is critical to meeting our energy demands through the engineering of an algal genotype that optimally matches the organism to its environment, because some traits desirable for fuel production may be biologically incompatible with other, co-evolved traits. In a similar vein, choosing strains that have evolved tolerance to pollutants might help sustain populations in deteriorating environments, whilst strains naive to pollution might be a more conservative option when assessing ecological risk to chemical pollutants. Engineering solutions in waste-water treatment plants might be improved if we could harness evolution’s power to help biodegrade persistent compounds (Brenner et al., 2008). Other environmental problems with limited engineering-oriented solutions could be tackled with evolutionary perspectives. For example, biocides may be applied to combat algal blooms, but it is notoriously difficult to predict the timing, duration and toxicity of algal blooms. A better understanding of the evolutionary dynamics of such systems, gained, for example, by tracking environmental change in real-time and linking those changes with environmental sources of natural selection, could help us predict the outbreaks of toxic algae.

Indeed, there is a growing need in many areas of environmental science to efficiently forecast ecosystem change across natural and human-induced gradients (Petchey et al., 2015) and to understand the consequences of such changes for ecosystem (and evosystem) services (Costanza et al., 1997; Rudman et al., 2017). This is particularly relevant for ecosystems that provide vital services to society, but are also sensitive to anthropogenic impacts. Predictions about complex ecological systems are challenging and require solid understanding of ecological and evolutionary mechanisms behind population growth, genetic and trait diversity, trait-environmental relationships, trade-offs, and community dynamics. Such principles are present in the environmental science literature, but are only sporadically applied to solve environmental issues.

It is possible that prevailing misconceptions about the pace and prevalence of evolution may be blocking the integration of evolution into the environmental sciences. First, the pace of evolutionary adaptation is not only set by the rate of mutations and the subsequent rate of increase of novel alleles in the population. Instead, the rate of adaptation, i.e. the increase in mean population fitness over time, is directly proportional to the genetic variance in a population that can respond to natural selection (Fisher, 1930). Evolution from such existing levels of heritable trait variation in a population can be much quicker and more predictable than expected based on evolution driven via new variants in the population that arise solely by mutation. Second, evolution is neither rare nor a special case. The challenge for environmental science is to determine the relative importance of evolution, either for causing or for ameliorating a particular environmental problem.

Overall, we argue that evolutionary principles are a useful resource for coming up with solutions to environmental problems. On the one hand, seemingly rational solutions might require some ‘evolution proofing’ to effectively anticipate and limit any potential negative impacts of evolution on the expected outcomes of our interventions. On the other hand, evolution itself can be a powerful design strategy for solving environmental problems. Design by directed evolution, for example, has made considerable progress developing novel enzymes, and configuring communities to perform specific functions that improve environmental conditions. Natural selection is a powerful force that can efficiently explore the combinatorial trait space that organisms could theoretically occupy. The trait space of living systems is replete with opportunities to solve environmental problems, and natural selection might often outpace our own ability to find these solutions. Perhaps a way forward is to relinquish our engineering hubris in favor of a problem solving strategy that is either informed by, or directed by, evolution. Environmental science has a rich history of interdisciplinarity. A stronger integration with evolutionary biology would improve our ability to address global societal challenges in general (Carroll et al., 2014), and environmental challenges in particular.

Box 1: The four forces of evolution

Mutation

Mutations are random, heritable changes in the sequence or structure of a gene. They include substitutions of individual bases in the DNA sequence, insertions and deletions of DNA fragments, and structural rearrangements of chromosomes. New variants of the same gene generated by mutation are referred to as alleles. Mutations can be neutral, meaning they do not affect the phenotype of their carrier, advantageous in specific environments, meaning they affect the phenotype such that it increases survival and/or reproduction, i.e. fitness, or deleterious in specific environments. For example, a mutation that confers resistance to a pesticide may be beneficial in an environment where the pesticide is present but detrimental in an environment where the pesticide is absent. Mutations are the ultimate source of genetic variation and provide the original resource for adaptive evolution and biological innovation.

Natural Selection

Natural selection is the process of unequal survival and reproduction among individuals due to differences in phenotype. Some individuals of the population are more likely to survive and reproduce because they have trait combinations that make them better at coping with the current environment than other individuals. Assuming that the phenotypic traits under selection are heritable, i.e. trait values are transmitted across generations, the favorable traits, which represent ‘good genes’, will be passed to the offspring. In this way, the frequency of the ‘good’ gene variants will increase in the population, leading to evolutionary adaptation.

Gene flow

Gene flow is the exchange of genetic material between populations. It occurs when individuals or their gametes migrate into a new population and reproduce. Gene flow can bring new alleles (i.e. genetic variants) into the receiving population and thereby influence the potential for this population to evolve. Gene flow can be maladaptive, and reduce the fitness of the local population, or adaptive. If migration is sufficiently high and migrant genes are not selected against, gene flow will homogenize allele frequencies and reduce genetic differences in the genetic composition of populations.

Genetic drift

Genetic drift is the stochastic change in allele frequencies over generations. It occurs because allele frequencies in populations can deviate by chance from those of the parental generation, due to the random sampling of gametes. It affects particularly small populations. It can lead to the loss of genetic variation and the accumulation of deleterious mutations and, as a result, constrain a population's adaptation to changing environmental conditions.

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References

Abdelghani, A. A., Tchounwou, P. B., Anderson, A. C., Sujono, H., Heyer, L. R., & Monkiedje, A. (1997). Toxicity evaluation of single and chemical mixtures of roundup, Garlon-3A, 2, 4-D, and syndets surfactant to channel catfish (Ictalurus punctatus), bluegill sunfish (Lepomis microchirus), and crawfish (Procambarus spp.). Environmental Toxicology and Water Quality: An International Journal, 12(3), 237–243.

Andersen, K. G., Rambault, A., Lipkin, W. I., Holmes, E.C., and Garry, R. F. (2020). The proximal origin of SARS-CoV-2. Nature Medicine. https://doi.org/10.1038/s41591-020-0820-9

Abrams, P. A., & Walters, C. J. (1996). Invulnerable Prey and the Paradox of Enrichment. Ecology, 77(4), 1125–1133.

Bell, G., & Gonzalez, A. (2009). Evolutionary rescue can prevent extinction following environmental change. Ecology Letters, 12(9), 942–948.

Bell, G., & MacLean, C. (2018). The search for “evolution-proof” antibiotics. Trends in Microbiology, 26(6), 471–483.

Bickham, J. W., Sandhu, S., Hebert, P. D., Chikhi, L., & Athwal, R. (2000). Effects of chemical contaminants on genetic diversity in natural populations: implications for biomonitoring and ecotoxicology. Mutation Research, 463(1), 33–51.

Brady, S. P., Monosson, E., Matson, C. W., & Bickham, J. W. (2017). Evolutionary toxicology: Toward a unified understanding of life’s response to toxic chemicals. Evolutionary Applications, 10(8), 745–751.

Brandenburg, K. M., Wohlrab, S., John, U., Kremp, A., Jerney, J., Krock, B., & Van de Waal, D. B. (2018). Intraspecific trait variation and trade-offs within and across populations of a toxic dinoflagellate. Ecology Letters, 21(10), 1561–1571.

Brenner, K., You, L., & Arnold, F. H. (2008). Engineering microbial consortia: a new frontier in synthetic biology. Trends in Biotechnology, 26(9), 483–489.

Briand, E., Escoffier, N., Straub, C., Sabart, M., Quiblier, C., & Humbert, J.-F. (2009). Spatiotemporal changes in the genetic diversity of a bloom-forming Microcystis aeruginosa (cyanobacteria) population. The ISME Journal, 3(4), 419–429.

Brüssow, H. (2020). The Novel Coronavirus - A snapshot of current knowledge. Microbial Biotechnology, doi.org/10.1111/1751-7915.13557.

Bull, J. J., & Collins, S. (2012). Algae for biofuel: will the evolution of weeds limit the enterprise? Evolution; International Journal of Organic Evolution, 66(9), 2983–2987.

Burford, M. A., Carey, C. C., Hamilton, D. P., Huisman, J., Paerl, H. W., Wood, S. A., & Wulff, A. (2019). Perspective: Advancing the research agenda for improving understanding of cyanobacteria in a future of global change. Harmful Algae. https://doi.org/10.1016/j.hal.2019.04.004

Burns, T. P. (1992). Adaptedness, evolution and a hierarchical concept of fitness. Journal of Theoretical Biology, 154(2), 219–237.

Cadier, M., Andersen, K. H., Visser, A. W., & Kiørboe, T. (2019). Competition-defense tradeoff increases the diversity of microbial plankton communities and dampens trophic cascades. In Oikos. https://doi.org/10.1111/oik.06101

Carroll, S. P., Jorgensen, P. S., Kinnison, M. T., Bergstrom, C. T., Denison, R. F., Gluckman, P., Smith, T. B., Strauss, S. Y., & Tabashnik, B. E. (2014). Applying evolutionary biology to address global challenges. In Science (Vol. 346, Issue 6207, pp. 1245993–1245993). https://doi.org/10.1126/science.1245993

Chakraborty, S., Pančić, M., Andersen, K. H., & Kiørboe, T. (2019). The cost of toxin production in phytoplankton: the case of PST producing dinoflagellates. The ISME Journal, 13(1), 64–75.

Chen, G., & Rynearson, T. A. (2016). Genetically distinct populations of a diatom co-exist during the North Atlantic spring bloom. In Limnology and Oceanography (Vol. 61, Issue 6, pp. 2165–2179). https://doi.org/10.1002/lno.10361

Chisti, Y. (2007). Biodiesel from microalgae. Biotechnology Advances, 25(3), 294–306.

Chisti, Y. (2008). Biodiesel from microalgae beats bioethanol. Trends in Biotechnology, 26(3), 126–131.

Cloern, J. E. (2018). Why large cells dominate estuarine phytoplankton. Limnology and Oceanography, 63(S1), S392–S409.

Connon, R. E., Geist, J., & Werner, I. (2012). Effect-based tools for monitoring and predicting the ecotoxicological effects of chemicals in the aquatic environment. Sensors, 12(9), 12741–12771.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R. G., Sutton, P., & van den Belt, M. (1997). The value of the world's ecosystem services and natural capital. Nature, 387(6630), 253–260.

Coutellec, M.-A., & Barata, C. (2013). Special issue on long-term ecotoxicological effects: an introduction. Ecotoxicology , 22(5), 763–766.

Czekalski, N., Radhika, S., Birtel, J., Matthews,B., Bürgmann, H. (2015). Does human activity impact the natural antibiotic resistance background? Abundance of antibiotic resistance genes in 21 Swiss lakes. Environment international, 81, 45-55.

Das, S., & Dash, H. R. (Eds.). (2019). Microbial Diversity in the Genomic Era. Elsevier.

Engering, A., Hogerwerf, L., and Slingenbergh, J. 2013. Pathogen-host-environment interplay and disease emergence. Emerging Microbes & Infections 2 (2): e5.

Feckler, A., Thielsch, A., Schwenk, K., Schulz, R., & Bundschuh, M. (2012). Differences in the sensitivity among cryptic lineages of the Gammarus fossarum complex. The Science of the Total Environment, 439, 158–164.

Fisher, M. C., Hawkins, N. J., Sanglard, D., & Gurr, S. J. (2018). Worldwide emergence of resistance to antifungal drugs challenges human health and food security. Science, 360(6390), 739–742.

Fisher, R. A. (1930). The genetical theory of natural selection. Clarendon Press.

Frank, S. A. (2011). Natural selection. I. Variable environments and uncertain returns on investment. Journal of Evolutionary Biology, 24(11), 2299–2309.

Gragnani, A., Scheffer, M., & Rinaldi, S. (1999). Top-Down Control of Cyanobacteria: A Theoretical Analysis. The American Naturalist, 153(1), 59–72.

Grimm, N. B., Foster, D., Groffman, P., Grove, J. M., Hopkinson, C. S., Nadelhoffer, K. J., Pataki, D. E., & Peters, D. P. C. (2008). The changing landscape: ecosystem responses to urbanization and pollution across climatic and societal gradients. Frontiers in Ecology and the Environment, 6(5), 264–272.

Gunderson, L.H., and Holling, C.S. (eds). 2002. Panarchy: understanding transformations in human and natural systems. Island Press, Washington, D.C., USA.

Hairston, N. G., Jr, Ellner, S. P., Geber, M. A., Yoshida, T., & Fox, J. A. (2005). Rapid evolution and the convergence of ecological and evolutionary time. Ecology Letters, 8(10), 1114–1127.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D’Agrosa, C., Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann, D., Lenihan, H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M., Steneck, R., & Watson, R. (2008). A global map of human impact on marine ecosystems. Science, 319(5865), 948–952.

Hendry, A. P. (2017). Eco-evolutionary Dynamics. Princeton University Press.

Hendry, A. P., & Kinnison, M. T. (1999). Perspective: The Pace of Modern Life: Measuring Rates of Contemporary Microevolution. Evolution; International Journal of Organic Evolution, 53(6), 1637–1653.

Hochmuth, J. D., De Meester, L., Pereira, C. M. S., Janssen, C. R., & De Schamphelaere, K. A. C. (2015). Rapid Adaptation of a Daphnia magna Population to Metal Stress Is Associated with Heterozygote Excess. Environmental Science & Technology, 49(15), 9298–9307.

Hoffmann, A. A., & Parsons, P. A. (1997). Consistent heritability changes under poor growth conditions. Trends in Ecology & Evolution, 12(12), 460–461.

Holdich, D. M., Reynolds, J. D., Souty-Grosset, C., & Sibley, P. J. (2009). A review of the ever increasing threat to European crayfish from non-indigenous crayfish species. Knowledge and Management of Aquatic Ecosystems, 394-395, 11.

Houle, D., Govindaraju, D. R., & Omholt, S. (2010). Phenomics: the next challenge.

Nature Reviews. Genetics, 11(12), 855–866.

Huisman, J., Codd, G. A., Paerl, H. W., Ibelings, B. W., Verspagen, J. M. H., & Visser, P. M. (2018). Cyanobacterial blooms. Nature Reviews. Microbiology, 16(8), 471–483.

Jankowiak, J., Hattenrath-Lehmann, T., Kramer, B. J., Ladds, M., & Gobler, C. J. (2019). Deciphering the effects of nitrogen, phosphorus, and temperature on cyanobacterial bloom intensification, diversity, and toxicity in western Lake Erie. Limnology and Oceanography, 64(3), 1347–1370.

Johnson, T. J., Halfmann, C., Zahler, J. D., Zhou, R., & Gibbons, W. R. (2016). Increasing the tolerance of filamentous cyanobacteria to next-generation biofuels via directed evolution. Algal Research, 18, 250–256.

Jones, K. E., Patel, N. G., Levy, M. A., Storeygard, A., Balk, D., Gittleman, J. L., & Daszak, P. (2008). Global trends in emerging infectious diseases. Nature, 451(7181), 990–993.

Jørgensen, P. S., Folke, C., & Carroll, S. P. (2019). Evolution in the Anthropocene: Informing Governance and Policy. Annual Review of Ecology, Evolution, and Systematics. https://doi.org/10.1146/annurev-ecolsys-110218-024621

Ju, F., Beck, K., Yin, X., Maccagnan, A., McArdell, C.S., Singer, H.P., Johnson D.R., Zhang, T. Bürgmann, H. 2019. Wastewater treatment plant resistomes are shaped by bacterial composition, genetic exchange, and upregulated expression in the effluent microbiomes. The ISME Journal 13 (2): 346–60.

Kahl, S., Kleinsteuber, S., Nivala, J., van Afferden, M., & Reemtsma, T. (2018). Emerging Biodegradation of the Previously Persistent Artificial Sweetener Acesulfame in Biological Wastewater Treatment. Environmental Science & Technology, 52(5), 2717–2725.

Kazamia, E., Riseley, A. S., Howe, C. J., & Smith, A. G. (2014). An Engineered Community Approach for Industrial Cultivation of Microalgae. Industrial Biotechnology, 10(3), 184–190.

Kennedy, D. A., & Read, A. F. (2018). Why the evolution of vaccine resistance is less of a concern than the evolution of drug resistance. Proceedings of the National Academy of Sciences of the United States of America, 115(51), 12878–12886.

Kimberly, D. A., & Salice, C. J. (2012). Understanding interactive effects of climate change and toxicants: importance of evolutionary processes. Integrated Environmental Assessment and Management, 8(2), 385–386.

Kim, S.-G., Joung, S.-H., Ahn, C.-Y., Ko, S.-R., Boo, S. M., & Oh, H.-M. (2010). Annual variation of Microcystis genotypes and their potential toxicity in water and sediment from a eutrophic reservoir. FEMS Microbiology Ecology, 74(1), 93–102.

Kiørboe, T., & Andersen, K. H. (2019). Nutrient affinity, half-saturation constants and the cost of toxin production in dinoflagellates. Ecology Letters, 22(3), 558–560.

Krakauer, D. C. (2011). Darwinian demons, evolutionary complexity, and information maximization. Chaos, 21(3), 037110.

Kristensen, T. N., Ketola, T., & Kronholm, I. (2018). Adaptation to environmental stress at different timescales. Annals of the New York Academy of Sciences. https://doi.org/10.1111/nyas.13974

Kueneman, J. G., Woodhams, D. C., Harris, R., Archer, H. M., Knight, R., & McKenzie, V. J. (2016). Probiotic treatment restores protection against lethal fungal infection lost during amphibian captivity. Proceedings. Biological Sciences / The Royal Society, 283(1839). https://doi.org/10.1098/rspb.2016.1553

Law, R. (1979). Optimal life histories under age-specific predation. The American Naturalist, 114, 399–417.

Lebret, K., Kritzberg, E. S., Figueroa, R., & Rengefors, K. (2012). Genetic diversity within and genetic differentiation between blooms of a microalgal species. Environmental Microbiology, 14(9), 2395–2404.

Leitwein, M., Duranton, M., Rougemont, Q., Gagnaire, P.-A., & Bernatchez, L. (2019). Using Haplotype Information for Conservation Genomics. Trends in Ecology & Evolution. https://doi.org/10.1016/j.tree.2019.10.012

Lewin, G. R., Carlos, C., Chevrette, M. G., Horn, H. A., McDonald, B. R., Stankey, R. J., Fox, B. G., & Currie, C. R. (2016). Evolution and Ecology of Actinobacteria and Their Bioenergy Applications. Annual Review of Microbiology, 70, 235–254.

Lewitus, A. J., Horner, R. A., Caron, D. A., Garcia-Mendoza, E., Hickey, B. M., Hunter, M., Huppert, D. D., Kudela, R. M., Langlois, G. W., Largier, J. L., Lessard, E. J., RaLonde, R., Jack Rensel, J. E., Strutton, P. G., Trainer, V. L., & Tweddle, J. F. (2012).

Harmful algal blooms along the North American west coast region: History, trends, causes, and impacts. Harmful Algae, 19, 133–159.

Li, D., Kong, F., Shi, X., Ye, L., Yu, Y., & Yang, Z. (2012). Quantification of microcystin-producing and non-microcystin producing Microcystis populations during the 2009 and 2010 blooms in Lake Taihu using quantitative real-time PCR. Journal of Environmental Sciences, 24(2), 284–290.

Lips, K. R., Brem, F., Brenes, R., Reeve, J. D., Alford, R. A., Voyles, J., Carey, C., Livo, L., Pessier, A. P., & Collins, J. P. (2006). Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. Proceedings of the National Academy of Sciences of the United States of America, 103(9), 3165–3170.

Liu, S., & Suflita, J. M. (1993). Ecology and evolution of microbial populations for bioremediation. Trends in Biotechnology, 11(8), 344–352.

Longdon, B., Brockhurst, M.A., Russell, C.A., Welch, J.J., and Jiggins, F.M. (2014). The evolution and genetics of virus host shifts. PLoS Pathogens 10 (11): e1004395.

Loria, A., Cristescu, M. E., & Gonzalez, A. (2019). Mixed evidence for adaptation to environmental pollution. Evolutionary Applications, 220, 1014.

Low-Décarie, E., Kolber, M., Homme, P., Lofano, A., Dumbrell, A., Gonzalez, A., & Bell, G. (2015). Community rescue in experimental metacommunities. Proceedings of the National Academy of Sciences of the United States of America, 112(46), 14307–14312.

Masseret, E., Grzebyk, D., Nagai, S., Genovesi, B., Lasserre, B., Laabir, M., Collos, Y., Vaquer, A., & Berrebi, P. (2009). Unexpected Genetic Diversity among and within Populations of the Toxic Dinoflagellate Alexandrium catenella as Revealed by Nuclear Microsatellite Markers. Applied and Environmental Microbiology, 75(7), 2037–2045.

Mbala-Kingebeni, P., Aziza, A., Paola, N.D., Wiley, M.R., Makiala-Mandanda, S., Caviness, K., Pratt, C.B. et al. 2019. Medical countermeasures during the 2018 ebola virus disease outbreak in the North Kivu and Ituri Provinces of the Democratic Republic of the Congo: A rapid genomic assessment. The Lancet Infectious Diseases 19 (6): 648–57.

McDonald, B.A., and Stukenbrock E.H. (2016). Rapid emergence of pathogens in Agro-Ecosystems: Global threats to agricultural sustainability and food security. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 371 (1709).

Melián, C. J., Matthews, B., de Andreazzi, C. S., Rodríguez, J. P., Harmon, L. J., & Fortuna, M. A. (2018). Deciphering the Interdependence between Ecological and Evolutionary Networks. Trends in Ecology & Evolution, 33(7), 504–512.

Monchamp, M.-E., Spaak, P., Domaizon, I., Dubois, N., Bouffard, D., & Pomati, F. (2018). Homogenization of lake cyanobacterial communities over a century of climate change and eutrophication. Nature Ecology & Evolution, 2(2), 317–324.

Mooij, P. R., Stouten, G. R., Tamis, J., van Loosdrecht, M. C. M., & Kleerebezem, R. (2013). Survival of the fattest. Energy & Environmental Science, 6(12), 3404–3406.

Morgan, A. J., Kille, P., & Stürzenbaum, S. R. (2007). Microevolution and ecotoxicology of metals in invertebrates. Environmental Science & Technology, 41(4), 1085–1096.

Oziolor, E. M., Bickham, J. W., & Matson, C. W. (2017). Evolutionary toxicology in an omics world. Evolutionary Applications. https://doi.org/10.1111/eva.12462

Paerl, H. W., Hall, N. S., & Calandrino, E. S. (2011). Controlling harmful cyanobacterial blooms in a world experiencing anthropogenic and climatic-induced change. The Science of the Total Environment, 409(10), 1739–1745.

Palmer, A. C., & Kishony, R. (2013). Understanding, predicting and manipulating the genotypic evolution of antibiotic resistance. Nature Reviews. Genetics, 14(4), 243–248.

Palumbi, S. R. (2009). Better evolution through chemistry: rapid evolution driven by human changes to the chemical environment. ACS Symposium Series, 1025, 333–343.

Pančić, M., & Kiørboe, T. (2018). Phytoplankton defence mechanisms: traits and trade-offs. Biological Reviews of the Cambridge Philosophical Society, 93(2), 1269–1303.

Pedersen, B., & Tuomi, J. (1995). Hierarchical Selection and Fitness in Modular and Clonal Organisms. Oikos, 73(2), 167–180.

Penczykowski, R.M., Laine, A-L., and Koskella, B. (2016). Understanding the ecology and evolution of host-parasite interactions across scales. Evolutionary Applications 9 (1): 37–52.

Petchey, O. L., Pontarp, M., Massie, T. M., Kéfi, S., Ozgul, A., Weilenmann, M., Palamara, G. M., Altermatt, F., Matthews, B., Levine, J. M., Childs, D. Z., McGill, B. J., Schaepman, M. E., Schmid, B., Spaak, P., Beckerman, A. P., Pennekamp, F., & Pearse, I. S. (2015). The ecological forecast horizon, and examples of its uses and determinants. Ecology Letters, 18(7), 597–611.

Reid, N. M., Proestou, D. A., Clark, B. W., Warren, W. C., Colbourne, J. K., Shaw, J. R., Karchner, S. I., Hahn, M. E., Nacci, D., Oleksiak, M. F., Crawford, D. L., & Whitehead, A. (2016). The genomic landscape of rapid repeated evolutionary adaptation to toxic pollution in wild fish. Science, 354(6317), 1305–1308.

Relyea, R., & Hoverman, J. (2006). Assessing the ecology in ecotoxicology: a review and synthesis in freshwater systems. Ecology Letters, 9(10), 1157–1171.

Roemhild, R., Gokhale, C. S., Dirksen, P., Blake, C., Rosenstiel, P., Traulsen, A., Andersson, D. I., & Schulenburg, H. (2018). Cellular hysteresis as a principle to maximize the efficacy of antibiotic therapy. Proceedings of the National Academy of Sciences of the United States of America, 115(39), 9767–9772.

Rudman, S. M., Kreitzman, M., Chan, K. M. A., & Schluter, D. (2017). Evosystem Services: Rapid Evolution and the Provision of Ecosystem Services. Trends in Ecology & Evolution. https://doi.org/10.1016/j.tree.2017.02.019

Rynearson, T. A., & Armbrust, E. V. (2000). DNA fingerprinting reveals extensive genetic diversity in a field population of the centric diatom Ditylum brightwellii. Limnology and Oceanography, 45(6), 1329–1340.

Sheehan, J., Dunahay, T., Benemann, J., & Roessler, P. (1998). A look back at the US Department of Energy’s aquatic species program: biodiesel from algae. National Renewable Energy Laboratory, 328. http://www.academia.edu/download/31018751/Biodiesel_from_algae_-

_USDOD_report.pdf

Shurin, J. B., Abbott, R. L., Deal, M. S., Kwan, G. T., Litchman, E., McBride, R. C., Mandal, S., & Smith, V. H. (2013). Industrial-strength ecology: trade-offs and opportunities in algal biofuel production. Ecology Letters, 16(11), 1393–1404.

Shurin, J. B., Burkart, M. D., Mayfield, S. P., & Smith, V. H. (2016). Recent progress and future challenges in algal biofuel production. F1000Research, 5. https://doi.org/10.12688/f1000research.9217.1

Smith, V. H., Sturm, B. S., Denoyelles, F. J., & Billings, S. A. (2010). The ecology of algal biodiesel production. Trends in Ecology & Evolution, 25(5), 301–309.

Stamm, C., Räsänen, K., Burdon, F. J., Altermatt, F., Jokela, J., Joss, A., Ackermann, M., & Eggen, R. I. L. (2016). Chapter Four - Unravelling the Impacts of Micropollutants in Aquatic Ecosystems: Interdisciplinary Studies at the Interface of Large-Scale Ecology. In A. J. Dumbrell, R. L. Kordas, & G. Woodward (Eds.), Advances in Ecological Research (Vol. 55, pp. 183–223). Academic Press.

Stockwell, C. A., Hendry, A. P., & Kinnison, M. T. (2003). Contemporary evolution meets conservation biology. Trends in Ecology & Evolution, 18(2), 94–101.

Strange, R. N., & Scott, P. R. (2005). Plant disease: a threat to global food security. Annual Review of Phytopathology, 43, 83–116.

Stukenbrock, E. H., & McDonald, B. A. (2008). The origins of plant pathogens in agro-ecosystems. Annual Review of Phytopathology, 46, 75–100.

Svoboda, J., Mrugała, A., Kozubíková-Balcarová, E., & Petrusek, A. (2017). Hosts and transmission of the crayfish plague pathogen Aphanomyces astaci: a review. Journal of Fish Diseases, 40(1), 127–140.

Thibodeau, G., Walsh, D. A., & Beisner, B. E. (2015). Rapid eco-evolutionary responses in perturbed phytoplankton communities. Proceedings. Biological Sciences / The Royal Society, 282(1814). https://doi.org/10.1098/rspb.2015.1215

Vörösmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S. E., Sullivan, C. A., Liermann, C. R., & Davies, P. M. (2010). Global threats to human water security and river biodiversity. Nature, 467(7315), 555–561.

Weber, M. G., Wagner, C. E., Best, R. J., Harmon, L. J., & Matthews, B. (2017). Evolution in a Community Context: On Integrating Ecological Interactions and Macroevolution. Trends in Ecology & Evolution, 32(4), 291–304.

Williams, L. M., & Oleksiak, M. F. (2008). Signatures of selection in natural populations adapted to chronic pollution. BMC Evolutionary Biology, 8, 282.

Xu, J., & Kiørboe, T. (2018). Toxic dinoflagellates produce true grazer deterrents. Ecology, 99(10), 2240–2249.

Yoshida, T., Hairston, N. G., Jr., & Ellner, S. P. (2004). Evolutionary trade-off between defence against grazing and competitive ability in a simple unicellular alga, Chlorella vulgaris. Proceedings of the Royal Society B - Biological Sciences, 271(1551), 1947–1953.

Yoshida, T., Jones, L. E., Ellner, S. P., Fussmann, G. F., & Hairston, N. G. (2003). Rapid evolution drives ecological dynamics in a predator–prey system. Nature, 424(6946), 303–306.

Zeng, X., Danquah, M. K., Chen, X. D., & Lu, Y. (2011). Microalgae bioengineering: From CO2 fixation to biofuel production. Renewable and Sustainable Energy Reviews, 15(6), 3252–3260.