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Eawag News

In focus

Aquatic biodiversity – a forgotten asset?

Editorial

Jukka Jokela, Member of the Eawag Directorate and Professor of Aquatic Ecology at the ETH Zurich.

Cause for concern: silent loss of freshwater diversity

The cumulative losses of biological diversity could cost EUR 14 trillion (14,000,000,000,000) in the year 2050. This recent EU estimate* is based on the assumption that biodiversity will continue to decline at the current rate. The figure is equivalent to more than half a million CHF for every minute of the next four decades – an enormous sum, which will largely have to be borne by taxpayers worldwide.

But the actual value of biodiversity is much higher than this estimate would suggest, for once it has been lost, diversity cannot be bought back. The loss of biodiversity involves more than the death of species. The value of biodiversity lies in ecosystem services – such as raw materials, drinking water, food, clean air and a healthy environment – which we take for granted, but without which human well-being would not even be possible. As biodiversity disappears, future generations will lose their natural capital and suffer serious deprivations. Freshwater ecosystems are particularly affected, since they have an unusually high level of biodiversity.

Switzerland is not immune to the global biodiversity crisis. Although only limited data are available, it is already clear that biological diversity has declined sharply in Swiss freshwaters. The reasons for this loss are complex – destruction and fragmentation of habitats, pollution of the environment, the spread of invasive species, competing interests among resource users and short-sighted policies. It is therefore no easy matter to halt the loss of biodiversity. There is a need for sustainable biodiversity management, which in turn calls for close political, scientific and economic coordination and continuous discussion at the national and international level. Also required is an in-depth analysis of why the targets defined in existing biodiversity agreements have not been met.

Recently, not least because of growing public awareness of this issue, some progress has been made. Switzerland is currently developing a national biodiversity strategy, which is due to be presented to Parliament before the end of the International Year of Biodiversity. In addition, revised legislation – including the Swiss Water Protection Act – is to come into force in 2011. The amendments, based on the parliamentary initiative concerning the use and protection of water resources, will lead to extensive restoration projects – which should also be beneficial to biodiversity. The aim now should be to deploy the available funds appropriately, to prioritize measures carefully and to promote dialogue among the various stakeholders. Here, Switzerland has the potential to play a pioneering role. Eawag – the Swiss Federal Institute of Aquatic Science and Technology – is closely involved in these efforts.

* Braat L., ten Brink P (Eds) (2008): The Cost of Policy Inaction (COPI): The case of not meeting the 2010 biodiversity target. (Final Report of a study commissioned by the European Commission).

Cover photo: Eawag technician Esther Keller studying plankton samples under the microscope. (© Eawag, Stefan Kubli)

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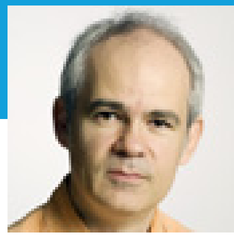
Aquatic biodiversity – a forgotten asset?



Mark Gessner, biologist and leader of the Ecosystems group in the Aquatic Ecology department; a member of the Swiss Biodiversity Forum since 2008 and of Diversitas (an international biodiversity science programme) from 2004 to 2008.

Biodiversity – facts, myths, prospects

Rivers, lakes and wetlands are particularly species-rich ecosystems. But this diversity is seriously threatened, and effective measures that ensure biodiversity persistence are urgently needed. To be successful, such efforts must be based on an integrative and comprehensive strategy. With the revision of the Swiss Federal Water Protection Act and the development of a national biodiversity strategy, Switzerland is sending clear signals in the right direction.

The concept of biodiversity has had an impressive career. Although only coined in the mid-1980s (see Box), the term now features prominently in both scientific and public debate. Influential figures have promoted the concept. They include evolutionary biologist and visionary E.O. Wilson, who served as the main editor of the landmark volume Biodiversity, published in 1988, and conservative ex-President of France Jacques Chirac. The unusually broad response to the concept arose largely because it was born of a crisis. From the outset, it was clearly recognized that biodiversity is rapidly declining. The global loss and degradation of habitat – from tropical rainforests to alluvial plains and dry grasslands in Switzerland – is well documented and omnipresent in the media. Current rates of species extinction are estimated to be 100 to 1000 times higher than the natural background rate. This comparison includes mass extinctions in Earth's history, such as the latest event 65 million years ago which wiped out the dinosaurs along with many other species. As a result of the current crisis, a political process started in the late 1980s and led to the adoption of the UN Convention on Biological Diversity in 1993. There are now 193 parties to this treaty. However, this has not yet resolved the crisis.

Freshwater diversity – remarkably rich and particularly threatened. Only a small fraction of the Earth's surface (0.3 %) is covered by lakes, rivers and marshes. Even in Switzerland, Central Europe's "water tower", little more than 4 % of the country's area is water. Likewise, surface freshwaters account for an extremely small portion of the world's water volume (< 0.001 % of the total volume, or 0.3 % of all freshwater), since 97 % of the total is in the oceans and the remaining 3 % is stored almost exclusively in glaciers, snowfields and ground water. Does the limited spatial extent of lakes, rivers and wetlands suggest that freshwaters make a negligible contribution to overall biodiversity? The opposite is true, in fact: freshwaters harbour around 40 % of the roughly 30,000 recognized fish species. This represents 20 % of all vertebrates worldwide, or 33 % of all vertebrates if other water-dependent species (e.g. amphibians) are added to the fishes. Scarcely less significant is the number of freshwater invertebrate species, of which over 100,000 have been described. Together with the vertebrates, they make up around 10 % of all known animal species. The mean species density (i.e. the number of species per unit area) is thus one to two orders of magnitude higher in lakes, rivers and marshes than on land or in the sea.

This high concentration of species, combined with the vital importance of water resources for humans and the relatively isolated nature of inland waters, means that freshwater biodiversity is particularly threatened. Hard facts on population trends and the loss of aquatic species are rare, however, despite increased data collection efforts in recent years. The number of freshwater species included in the IUCN Red List of Threatened Species has risen from about 2000 to more than 6000 over the last 7 years. However, these figures reflect primarily an expanded coverage of species and regions, rather than actually documented population changes. Estimates from North America indicate that extinction rates are considerably higher for freshwater than for terrestrial or marine species (Fig. 1) [1]. The same conclusion is also implied

Biodiversity – more than just species diversity

According to the UN Convention, biological diversity, or biodiversity, comprises:

- species diversity: the variety of living organisms,
- genetic diversity: the variability of genetic material,
- habitat diversity: the variety of natural habitats,
- functional diversity: the various functions of organisms, habitats and genetic information within ecosystems and of benefit to humans.

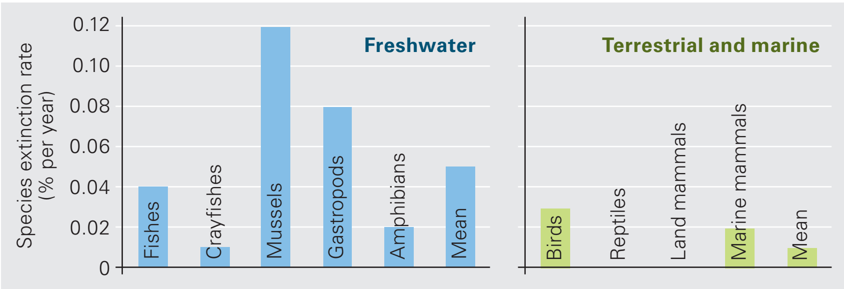


Fig. 1: Extinction rates are considerably higher for freshwater than for terrestrial and marine fauna (from [1]).

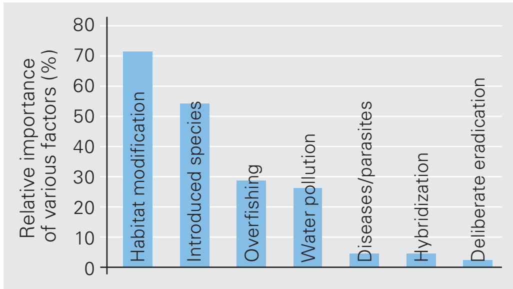


Fig. 2: The loss of fish species worldwide can be attributed to a variety of factors (from [3]).

by the 2008 Living Planet Index published by the WWF, although the incomplete reporting of methodology falls short of meeting the standards of scientific investigation. This limitation aside, the population trends shown by the freshwater index from the early 1980s onwards are clearly worse than for marine or terrestrial ecosystems. Among freshwater organisms, fish are the best studied group (see article by Ole Seehausen on p. 18). In the case of fish – unlike for birds – a rapid loss of species has only been documented since the end of the 19th century, when rivers, lakes and wetlands were first significantly affected by engineering measures. One such major intervention in Switzerland was the Jura Waters Correction, undertaken between 1868 and 1891. By today, 8 of the 55 fish species (including lampreys, and counting whitefish and some taxa as single species) that are listed by the Swiss Federal Office for the Envrionment have become extinct – mainly those with complex habitat requirements and migratory behaviour.

Anthropogenic causes of declining biodiversity. Various factors are responsible for the loss of freshwater biodiversity (Fig. 2) [2, 3]. But ultimately all the causes, apart from climate change and, in some cases, the introduction of alien species, are related to human uses of surface waters and surrounding land. In industrialized countries, there have been marked improvements in levels of water pollution caused by municipal wastewater, nutrients and some chemicals (see article by Piet Spaak on p. 25). Yet in many places – even at the heart of Europe – water pollution remains a key problem, owing not only to a lack of infrastructure and financial resources but also to ignorance and the unabated increase in the number and volumes of synthetic substances produced and released into the environment. While overexploitation of freshwater biodiversity is now a less significant factor in Europe, it remains an important stressor in many other regions of the world, especially in Asia, and also in tropical areas of other continents.

Also widespread, and particularly critical in Switzerland, are alterations of the hydrological regime, which are often extensive and literally far-reaching. In the case of rivers and their floodplains, this problem is at least generally acknowledged, though still unresolved in view of the numerous conflicts over hydropower generation, land use, etc. In contrast, the impacts of widespread water level regulation on biodiversity in the littoral zones of lakes are only beginning to be recognized by water managers. Changes in hydrological regimes often lead to the destruction of habitats. They are frequently associated with a wide variety of direct engineering measures, including structures within or on surface waters (e.g. dams, embankments, run-of-the river hydropower plants, culverts and sills) as well as developments in riparian zones and floodplains, which are a key problem for biodiversity (see article by Martina Bauchrowitz on p. 8). Here, viable concepts promoting the conservation of biodiversity while enjoying broad support have yet to be devised. This is true in Switzerland and in other industrialized countries, in spite of increased surface water restoration efforts. In the Canton of Zurich, for example, 27 % of its 3615 km of total river length still run underground. Many other river engineering measures lead to longitudinal fragmentation and to disconnection of rivers from their floodplains and sometimes also from the associated aquifer. The consequences of these measures for biodiversity may extend well beyond modification at the local scale. While intentional or inadvertent introductions of animal and plant species often are not immediately disastrous, the increasing presence of alien species does make it more likely that some will eventually have dramatic impacts on aquatic biodiversity (see article by Kirstin Kopp on p. 22). Such impacts have been documented on every continent. A common myth is that alien species can only become predominant in degraded habitats. In a rainforest stream in Papua New Guinea, for example, three exotic fish species displaced seven of the nine native fish species within only a few years and reduced the numbers of the two surviving species to a small fraction of the total (Fig. 3) [4]. As a landlocked country, Switzerland is less exposed to invasions by alien species than many other countries. However, owing to the extensive man-made interconnections of European waterways, and misguided political decisions such as construction of the Rhine-Main-Danube Canal, alien species are increasingly reaching Swiss waters after a certain delay. This risk has not been taken seriously to date.

An important factor superimposing all other stresses on aquatic biodiversity is climate change. In future, this will increasingly affect not only hydrological and temperature regimes but also biogeochemical conditions, such as oxygen saturation, and interactions between organisms. Of particular concern in this country is the fact that direct impacts of climate change are to be

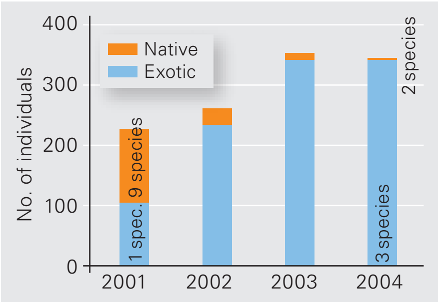


Fig. 3: In a mountain stream in the rainforest of Papua New Guinea, seven of originally nine native fish species were displaced within a few years by three introduced fish species (from [4]).

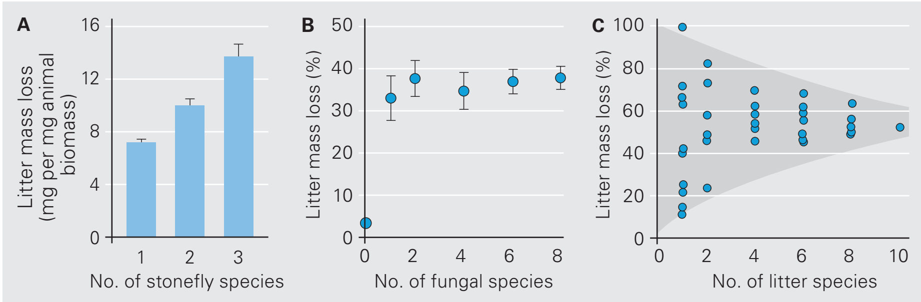


Fig. 4: Effects of changes in biodiversity on leaf litter decomposition, an important ecosystem process in streams. A: An increase in the species number of leaf-shredding stonefly larvae increases decomposition rate (from [8]). B: In contrast, decomposition rate is not affected by the species richness of litter-decomposing fungi (from [7]). C: A decrease in the variability of decomposition rate with increasing richness of litter species (i. e. riparian vegetation) illustrates the portfolio effect (from [9]).

expected increasingly at higher altitudes, where the overall impact of human activities has previously been less severe than in the Swiss Plateau.

Is aquatic biodiversity useful? The concept of ecosystem services. In western culture, the preservation of biodiversity and its development potential is a moral imperative and hence a social obligation. In addition to this ethical argument, the question arises to what extent individuals and society take benefit from biodiversity. The concept of ecosystem services, as set out in the Millennium Ecosystem Assessment coordinated by UNEP, offers a suitable framework for answering this question. Four types of ecosystem services are distinguished:

- ► *Provisioning services* are resources provided by nature. These include clean water, but also goods such as fish and other foodstuffs, or natural remedies.
- ► *Regulating services* include the self-purification of natural waters, the improvement of water quality in general, the regulation of floods, drought and extreme temperatures, and the sequestration of organic carbon.
- ► *Cultural services* encompass recreational, aesthetic, spiritual and other non-material benefits. For a tourist country such as Switzerland, these often translate directly into monetary values.
- ► Lastly, *supporting services* – i. e. ecosystem processes such as the production of biomass, decomposition of organic matter and other biogeochemical transformations, many of which are performed exclusively by microorganisms (see article by Helmut Buergmann on p. 12) – which provide the basis for the other three types of services.

Synergies arising from biodiversity? Given the importance of ecosystem processes for ecosystem services, the question whether ecosystem process rates are influenced by biodiversity has been extensively studied in recent years, including by researchers at Eawag [5, 6]. Multiple experiments have shown that in some cases process rates are indeed strongly dependent on biodiversity (Fig. 4A). However, there is also evidence suggesting that the notion that ecosystem process rates are invariably affected by biodiversity is a myth (Fig. 4B). This conclusion remains tentative, however, since studies to date have almost exclusively involved strongly simplified model systems, and initial findings suggest that synergistic effects are observed more frequently in model systems of greater complexity. Clearly, there is a need here for future research, first to analyse progressively more realistic model systems and secondly to explore the critical connection between ecosystem process rates and services of direct benefit to humans.

The insurance effect of biodiversity. Apart from the magnitude of process rates, their variability may be highly important for their utility to humans. As species richness or genetic diversity increases, it becomes more likely that certain species or genotypes will respond differently to changes in environmental conditions. This principle can also be relevant in technical systems such as wastewater treatment plants (see article by Eberhard Morgenroth on p. 15). Moreover, it is more likely that the role of some species or genotypes lost from an ecosystem will be assumed by other species. The most important mechanism underlying this insurance function is the so-called portfolio effect [7, 9]. This refers to the fact that the variability of process rates tends to decrease with increasing diversity of species or genotypes in a community or population, because the influence of extreme species is dampened (Fig. 4C). Thus, by analogy with the stock market, community or population diversity will prevent both huge gains (i. e. high process rates) and excessive losses (i. e. low process rates). Experiments with microorganisms and leaf litter from riparian vegetation have demonstrated this theoretically compelling relationship also empirically [7, 9]. The portfolio effect increases the reliability that processes operate at an average rate. But this by no means implies that, in a given situation, increased diversity will always lead to enhanced system functioning.

What about the future? In the face of a growing world population, rising affluence among broad sections of the population, and numerous conflicts surrounding the use of water and water bodies, the prospects for freshwater biodiversity conservation are dire. As part of a transdisciplinary collaboration between Diversitas (an international biodiversity science programme) and the Global Water Systems Project (GWSP), we have begun to analyse global water security from both a human and biodiversity viewpoint at a level of spatial resolution not possible before. Our analysis shows, as expected, that investments in water infrastructure in developed countries ensure human water security. But it also suggests that these investments are frequently counterproductive (e.g. river engineering projects) or at least insufficient to ensure biodiversity conservation. Therefore, effective protection of freshwater biodiversity calls for a completely new approach to water management, one that integrates requirements for biodiversity as a key component. This new way of thinking has already started to find its way into modern approaches to flood protection.

Biodiversity in 2010: much talk, but limited action. The UN's declaration of 2010 as the International Year of Biodiversity has further enhanced the issue of biodiversity as a focus of political and public attention. This notwithstanding, the declared target of significantly reducing the rapid decline of biodiversity by the year 2010 has been clearly missed [10]. Extension of the deadline to 2020 will not be effective either, unless fundamental deficiencies are addressed at many levels. This starts with awareness of the problem; the true extent of changes in freshwater biodiversity might well be underestimated even among experts. Is this why Switzerland's National Parliament approved the development of a biodiversity strategy only in 2008, long after other European countries had done so? With a national strategy and agenda clearly defined, the information base on biodiversity, which to date has been woefully inadequate even for countries like Switzerland, could be significantly improved soon. This would greatly benefit effective biodiversity management. However, given the current enormous information gaps on species numbers, population trends, genetic diversity, etc., biodiversity management will have to deal with considerable uncertainties also in the future. This makes it all the more important to develop and apply workable concepts for understanding the extent, causes and consequences of declining biodiversity – a challenge to be taken up by science – and to derive effective water management plans on this basis. This means, for example, considering the catchment as the fundamental spatial unit when designating protected areas that comprise terrestrial and aquatic habitats. It is evident that substantial financial resources will also be needed. But what is required most is a broad-based will to initiate fundamental changes. Only such a commitment will enable shifts in priorities that accord appropriate weight to freshwater biodiversity within integrative land management programmes.

Given its abundant water resources, topography and connecting role between biogeographical regions, Switzerland has responsibility in Europe especially for freshwaters and their biodiversity. A draft of Switzerland's national biodiversity strategy is due by mid-2010 (see article by Evelyne Marendaz Guignet on p. 28); it provides an opportunity to define the conservation and promotion of biodiversity as a key cross-cutting task. A further step in the right direction is the revised national legislation based on the recent parliamentary initiative for the "Protection and Use of Water Bodies". The new legislation is due to come into effect in 2011 and will lead to extensive river restoration measures in the coming decades. The success of these instruments will largely depend on the extent to which comprehensive, cross-sectoral options for action can be defined. ○○○

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Influence of habitat diversity on species richness

Swiss rivers are highly degraded as a result of engineering measures, with monotonous habitats fragmented by artificial barriers. But biodiversity is associated with richly structured ecosystems, such as braided channels or alluvial zones. So what can be done to promote diversity, particularly of fish fauna? We discussed this question with fish ecologist Armin Peter and floodplain expert Klement Tockner.

Klement Tockner, who frequently gives presentations to young people in schools, has been amazed to hear how most of the students respond when they are asked which picture they prefer – a regulated or a natural river. They choose the photo of a straightened river channel. "It's what they're familiar with," Tockner concludes. "It appeals to their aesthetic sense – the symmetry, the linearity." In fact, the young people's verdict is not that surprising, given the massive changes which Switzerland's formerly diverse river network has undergone over the past couple of centuries. And what happens when he only shows the photos after talking about the value and functions of natural waters and explaining the importance of habitat diversity? Then they choose the other picture. Obviously, says Tockner, the young people understand that the morphological status of a watercourse has significant effects on aquatic communities. This, Armin Peter adds, is particularly true of fish fauna. The more uniform a river, the lower the diversity of fish species: "Fish are good indicators."

"Fish are good indicators," says the fish ecologist Armin Peter, who leads the Restoration Ecology group in the Fish Ecology and Evolution department at Eawag.

Val Roseg alluvial landscape – one of Switzerland's few remaining natural alluvial plains. Today, it is estimated that only 54 % of Switzerland's rivers are in a near-natural state. The aim of large-scale river modification projects was to reclaim land for agriculture and development, to improve flood defences and to expand hydropower generation. In the process, streams and rivers were channelized and culverted (enclosed in pipes), which dramatically shortened river stretches and reduced channel widths (see the Box on p. 10). In addition, streams were heavily fragmented by short culverts at road crossings. After being straightened, many regulated watercourses showed a tendency to erode (channel deepening) and were stabilized by submerged sills and transverse structures. In fact, some major European rivers were deliberately deepened for navigation purposes. "Today, it's difficult to find any natural watercourses in Switzerland and Europe, so we're very lucky to be able to carry out research on the Roseg river in the Upper Engadine," says Tockner. During his time at Eawag, Tockner was involved in a wide-ranging project investigating the alpine alluvial landscape of Val Roseg. Because of their dynamics and habitat diversity, he explains, natural alluvial zones are sites of unique biological diversity. This is partly due to the close links with the associated groundwater and the surrounding land. Dynamic ecosystems such as alluvial zones promote evolutionary processes and thus play a key role in the development of biodiversity. Compared with terrestrial systems, as Peter points out, freshwaters only account for 4.1 % of the total area of Switzerland, but they make a disproportionate contribution to the country's overall biodiversity – and loss of species.

Artificial barriers impeding fish passage. "Particularly at risk," says Tockner, "are groups of organisms with complex life cycles, such as those which need both aquatic and terrestrial habitats to complete their life cycle." Examples include amphibians and aquatic insects. In the case of aquatic insects, conservation and restoration activities mainly focus on the larval stage, although in fact the quality of the riparian and alluvial habitat during the brief adult flight period is usually more critical to the survival of populations.

Complex life cycles are also common among fish, e.g. in species such as salmon, sea trout or sturgeon which migrate between saltwater and freshwater. Peter comments: "No long-distance migrants – apart from the eel – can now be found in Swiss rivers." The rivers are so heavily fragmented by barriers that fish can no longer migrate upstream to their spawning grounds. Also affected by barriers are fish which swim shorter distances: in the Töss river, for example, Eawag researchers counted 23 fish species below the 6-m-high weir at the Freienstein hydropower plant, but only 12 above this barrier. "Or take the case of the Goldach river in Canton St Gallen," says Peter. "Between Lake Constance and the first artificial barrier, we observed 11 fish species; above it, there were only 2 fish species." Many more examples could be cited, clearly demonstrating the abrupt decline in biodiversity caused by artificial barriers.

"Groups of organisms with complex life cycles are particularly at risk," says the limnologist Klement Tockner. Having carried out research at Eawag from 1996 to 2007, he is now Director of the Leibniz Institute of Freshwater Ecology and Inland Fisheries in Berlin.

Too steep for fish to climb. In addition, as a result of deepening, numerous channelized stretches have become disconnected from their tributaries, making exchanges between the main and side channels impossible. Thus, 46 of 54 tributaries of the Sitter river were found to be inaccessible for bullheads. Peter explains: "This is because bullheads are poor swimmers which move along the river bed and aren't able to manage the steep climb into the tributaries of the Sitter." A good example of a successful restoration project is the mouth of the Liechtensteiner Binnenkanal. From 1931 to 1943, all 12 tributaries of the Rhine existing in the principality at that time were combined into this artificial channel. Before the restoration project, there was a drop of 4–5 m where the channel entered the Rhine. In the 1990s, only 6 fish species could still be found in the channel. The Liechtenstein government and the neighbouring communes therefore decided to reshape the channel mouth, and in 2000 – just 3½ years after the restoration work – 16 fish species were detected.

"Conversely," Tockner emphasizes, "near-natural side channels in particular have an enormous potential for the recolonization of habitats." As well as stream mouths, interconnected alluvial waters, islands, gravel banks and woody debris are among the key habitats which enhance the potential for regeneration of a river landscape and thus contribute to the success of restoration efforts.

Numerous problems caused by hydropower plants. While low weirs tend to impede the upstream movement of fish, larger structures – specifically hydropower plants – are barriers to both upstream and downstream movements. To address this problem, fish ladders are installed at these sites. Peter says: "Nowadays, for upstream movement, the attraction flow can be adjusted so well that the fishways are effective." However, there are still a lot of fish ladders which do not meet the latest ecological requirements. In addition, these migration aids are of no use for downstream movement because fish swimming with the main flow enter the turbines, where larger fish in particular will perish. This problem cannot be avoided even by the installation of near-natural fish bypasses, such as those built on the Aare at Ruppoldingen, Winznau, Schönenwerd or Rupperswil.

As well as causing fragmentation, hydropower plants are detrimental to aquatic ecology in other ways: sediment dynamics and the temperature regime are altered, there may be considerable fluctuations in flows (hydropeaking) and residual downstream flows are frequently inadequate.

Eawag has shown, for example, that in river reaches affected by hydropeaking significantly fewer juveniles are found than in reaches not subject to variable flows. This means that the former reaches can no longer fulfil their function as breeding waters. In addition, if a residual flow stretch is compared with an upstream stretch, it becomes clear to what extent biodiversity is affected by low flows: in 1989, 14 different fish species were found in the Sarner Aa river above the Wichelsee, with only 8 species in the residual flow stretch below the reservoir. Moreover, fish biomass decreased from around 130 to 10 kg per hectare.

Are restoration projects worthwhile? The aim of the UN Convention on Biological Diversity was to halt the decline in biodiversity by 2010 – a target which has not been met. "But what's worse," says Tockner, "is that for many species – and aquatic groups in particular – we don't even know what the trend is." A sound data base on biodiversity status and changes is thus urgently required, as is a rigorous analysis of the reasons for the failure to meet the 2010 target.

In December 2009, the Federal Council adopted the Swiss Parliament's initiative on the protection and use of water resources, which includes amendments to the Water Protection, Hydraulic Engineering and Energy Acts and also to the Act on Agrarian

Ample room for the Posterior Rhine at Rhäzüns – a diverse alluvial landscape with gravel banks and woody debris. But the positive structural characteristics of this former alluvial zone are undermined by the hydropeaking regime of the Posterior Rhine.

Land Law. These will come into effect in 2011. The goal is to reduce the adverse impacts of hydropower operations and to promote the restoration of natural waters. In the hydropower sector, operators will be responsible for the planning and implementation of measures (e. g. mitigating hydropeaking and altered sediment regimes, ensuring fish passability) over the period up to 2030. The funds required – approx. CHF 50 million a year – are to be raised by a surcharge of no more than 0.1 cents per kWh on high-voltage network transmission costs.

In the area of restoration, responsibility lies with the cantons. They are to develop a comprehensive rehabilitation programme for the next 20 years, with the federal government providing CHF 40 million a year in funding. Peter comments: "Even though there is currently a global trend towards restoration, the consistency and breadth of this programme certainly mean that Switzerland is playing a pioneering role." Experience accumulated from restoration projects which have already been completed should now be analysed, and priority projects identified for the future. Here, Tockner emphasizes, it is important to take a cross-sectoral approach: "Representatives of the agricultural, conservation, power generation and flood protection sectors must get together with hydraulic engineers and ecologists to harmonize competing objectives."

Alluvial zone protection *versus* promotion of small hydropower. Biodiversity strategies in general still have to contend with the wide variety of interests in the use of water resources. In Germany, numerous measures have been defined so as to restore natural waters to a good ecological status by 2015. According to Tockner, the intentions are good, but the goal is frequently unattainable – partly because of conflicting developments. In Germany, as in Switzerland, the expansion of small hydropower plants is being promoted, and the last near-natural rivers are being engineered and fragmented as a result – "at the expense of biodiversity in particular!" says Tockner.

The value of biodiversity. At this point, the concept of ecosystem services comes into play (see also the article by Mark Gessner on p. 4). According to the UN Millennium Ecosystem Assessment, these services can be divided into four categories – provisioning, regulating, cultural and supporting. "Biodiversity is indispensable for each of these categories," says Tockner. And just as efforts have been made to quantify the benefits provided by ecosystem services, methods have been developed to calculate the value of biodiversity. Usually, however, what is estimated is the economic value – i.e. the value of biodiversity is taken to depend not just on its intrinsic (e.g. ecological) characteristics, but to a large extent on the economic context of the evaluation. As Peter explains, this would mean that economically desirable fish, for example, contribute more to the economic value of biodiversity than small species of no fishery importance. Contrary to these considerations, however, biodiversity also has an intrinsic value which cannot be quantified. Nonetheless, as Peter and Tockner agree, efforts to put a figure on the value of biodiversity and ecosystem services do help to provide a basis for decisions on future water management policy.

Key figures on the state of Swiss waters

- 65,000 km river network
- Watercourses in poor condition: 40 % in Central Plateau, 80 % in urban areas
- Adversely affected by hydropower generation: over 90 % of all usable waters
- Artificial barriers over 50 cm high: approx. 100,000
- Artificial barriers under 50 cm high: several hundred thousand
- Man-made structures (e.g. dams and power plants): 8841
- Mean unobstructed stretch: 650 m
- Barriers per river-kilometre: 2 (Canton Bern) to 11 (Canton Zurich)
- Barriers in the Töss river along a 59.7 km stretch from source to mouth: 568 artificial as well as just 35 natural barriers
- Hydropower plants >300 kW: 538
- Small hydropower plants: approx. 1060
- Extinct fish and lamprey species: 8 species (= 14.5 % of fish fauna), excluding whitefish
- Extinct whitefish species: over 30 % of known species

New management approach: not just conservation, but manipulation. One strategy adopted for biodiversity conservation is the designation of minimally degraded waters as protected sites. However, since many of our waters have lost their natural dynamics as a result of human interventions, another possibility, in Tockner's view, is to "redynamize" natural waters by manipulative measures – an approach which goes some way towards restoration. "A good example is the Spöl in the Engadine," says Peter. Since 1970, the water in this mountain stream has been impounded and used for power generation. But below the dam, the Spöl was severely affected by the new, somewhat monotonous and restricted flow regime. For this reason, since 2000, a more dynamic regime has been restored: now, several times a year, artificial floods are generated – with favourable effects on the river fauna.

A turning point for water management. In Switzerland and Germany today, more waterbodies are being restored than straitjacketed – an encouraging reversal of the previous trend. With the comprehensive restoration measures which are to be undertaken in Switzerland from 2011 – based on the parliamentary initiative on the protection and use of water resources – this approach will be consistently pursued. Armin Peter and Klement Tockner are convinced that, if resources are appropriately deployed, the country's waters can be successfully restored to a near-natural state. And they are sure that biodiversity will also ultimately benefit from these measures. At the same time, as well as financial resources and sound methods, a certain amount of patience will be required.

Martina Bauchrowitz

Helmut Buergmann, geoecologist and leader of the Microbial Ecology group in the Surface Waters department.

Microbial diversity – unseen variety

The diversity of microorganisms exceeds that of higher organisms in many ecosystems. In addition, microorganisms play a key role in vital ecosystem processes. Should microbial diversity therefore receive more attention – or even be protected?

The International Year of Biodiversity has focused attention on efforts to safeguard the diversity of life on earth. While the emphasis is on the conservation of animal and plant species, the term "biodiversity" – by definition – covers the whole spectrum of living organisms, and thus also microorganisms. This group includes in particular the prokaryotes, i. e. bacteria and archaea. An excellent opportunity to reflect on the role and significance of microbial diversity.

Microorganisms: more diverse than higher forms of life. The fact that microorganisms are a highly diverse group is evident, for example, from the gene sequences of ribosomal RNA (rRNA). Along with proteins, rRNA makes up the ribosomes – the organelles within the cell which are the site of protein synthesis in all organisms. Comparison of known rRNA sequences indicates that they vary more widely among prokaryotes than among eukaryotes (Fig. 1). Since many members of the eukaryote domain – given their size and unicellular nature – must also be classified as microorganisms, the genetic diversity of microorganisms overall is far greater than that of higher forms of life (plants, fungi, animals).

Taking only prokaryotes into account, it is estimated that more than 160 species occur in a millilitre of seawater, and over 8000 in a gram of soil [1]. However, it is difficult to determine the true extent of prokaryotic diversity for the earth as a whole. Calculations suggest that there are between 35,000 and 10^9 prokaryote species worldwide. But because the definition of species is based on comparison of a single gene – here, on rRNA gene similarity – this also means that there may be considerable genetic diversity within the species thus defined.

In the rest of this article, the term "microorganisms" always refers to the prokaryotes (including archaea).

The molecular revolution. Up until the 1980s, the topic of microbial diversity was in fact considered to have been essentially exhausted. With the methods available at the time, based on the culturing and isolation of microorganisms, the existing diversity seemed to have been fully documented. Several thousand species were known, with freshwater ecosystems appearing to harbour largely the same microorganisms as terrestrial ones. Doubts were prompted solely by the observation that only a fraction of the microorganisms countable under the microscope would ever grow on nutrient media. Only with the use of culture-independent molecular biological methods (Fig. 2) did it become clear that microbial diversity had been significantly underestimated. Numerous new species – even dozens of prokaryotic groups – were discovered which had not previously been cultured.

It soon also became clear that there were fundamental differences between aquatic and terrestrial ecosystems in the composition of microbial communities.

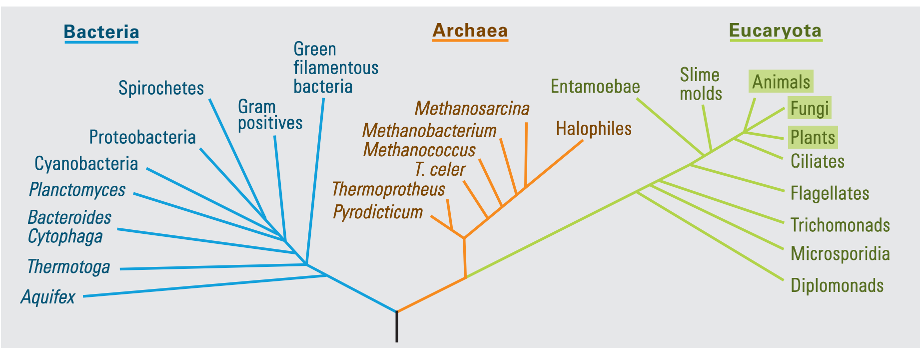


Fig. 1: A phylogenetic tree of life based on genetic information from ribosomal RNA (rRNA) [2]. Genetic diversity among prokaryotes exceeds by far that of higher organisms (plants, fungi, animals). This scheme is highly simplified – according to the latest research, bacteria alone can be classified into 50 separate subgroups.

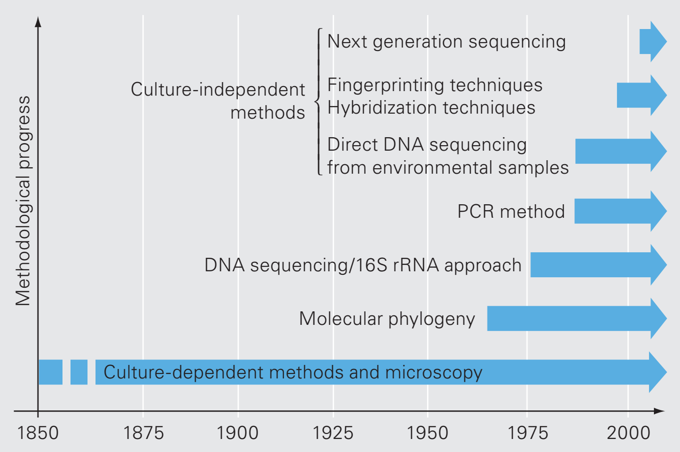
Today, the techniques of molecular biology are an integral part of environmental microbiology [3]. A key method is the polymerase chain reaction (PCR), in which billions of copies of sections of genetic material are produced which can subsequently be analysed using a variety of other methods – e. g. denaturing-gradient gel electrophoresis (Fig. 3). But despite the methodological advances, microbial diversity in complex ecosystems has yet to be fully described.

Key role in ecosystems. Microorganisms play a key role in the functioning of all ecosystems, and specifically aquatic ecosystems. They are intimately involved in biogeochemical cycling (e. g. of carbon, nitrogen, sulphur and oxygen) and thus directly influence chemical conditions in surface waters. For example, under natural conditions, nitrogen fixation, sulphate reduction or methanogenesis are processes mediated exclusively by the biological activity of prokaryotes.

A particularly striking example of microbial activity is to be found in the East African Lake Kivu, which has been studied by Eawag (see Fig. 3). Over a period of millennia, methanogenic archaea have caused high concentrations of the greenhouse gas methane to build up in the depths of the lake. Now, methane-oxidizing microorganisms (known as methanotrophs) in the upper water layers are preventing methane from being released into the atmosphere (Pasche et al., in preparation). Interestingly, it was found that in addition to the fairly widespread methanotrophic bacteria, which break down methane with the aid of oxygen, Lake Kivu also harbours a population of anaerobic methanotrophic archaea, which use sulphate instead of oxygen.

In addition, microorganisms play a vital part in the decomposition of organic matter. In a current project, for example, Eawag is investigating how microorganisms degrade chitin, one of the most abundant biopolymers in aquatic systems. Chitin is found in the exoskeletons of zooplankton and also in fungi and certain algae. Initial results show that the activity of chitin-degrading organisms is focused on particles suspended in water and on sediment. However, the diversity of the microorganisms is limited – apparently, specialists are responsible for chitin degradation in freshwater.

Fig. 2: Advances in microbiological methods since 1850. Molecular techniques have only been developed over the past few decades (modified from [3]).



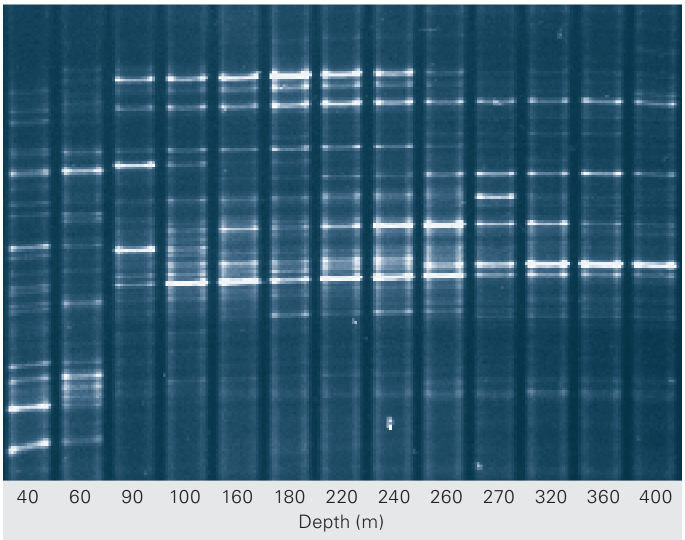


Fig. 3: Denaturing-gradient gel electrophoresis (DGGE) profile of the bacterial community of Lake Kivu (East Africa). The individual bands correspond to bacterial species, with band intensity indicating the relative abundance of each species. The resolution of DGGE is, however, limited – only the more abundant species are represented (from Pasche et al., in preparation).

The fact that the composition of the microbial community may determine the effects of environmental changes is demonstrated by another study. This study is concerned with those alpine streams which are particularly affected by climate change. Initial findings suggest that, in different streams, microbial enzymatic activities react differently to environmental changes, thus in turn influencing the chemical properties of the water.

In addition to their role in material cycles, microorganisms serve various other functions – as parasites and pathogens, as competitors for nutrients and, at the same time, as food sources for higher organisms.

Microbial diversity – purely a function of the environment? Microorganisms are thus highly diverse and serve important functions within the ecosystem. Why then is so little attention paid to microbial diversity in current discussions of biodiversity and in conservation efforts? There would appear to be two main reasons: firstly, microbial diversity – precisely because of the microscopic dimensions of these organisms – does not impinge on our everyday experience. Secondly, it is still widely assumed among scientists that microbial community composition is purely a function of environmental conditions – a view which goes back to what is known as the Baas Becking hypothesis: "Everything is everywhere, but the environment selects". This hypothesis, developed by the Dutch microbiologist Lourens Baas Becking (1895–1963), maintains that all prokaryotes are universally present – i. e. cosmopolitan – in a latent form, and that environmental conditions determine which species predominate [4]. If this concept is taken to be correct, it means that microbial species, being ubiquitous, can never become extinct and it essentially makes no sense to speak of conserving such species; at any rate, it suggests that microbial diversity can be assured by protecting habitats.

Cosmopolitan *versus* endemic species. More recent research, however, has increasingly cast doubt on the universal validity of the Baas Becking hypothesis – particularly in the case of aquatic ecosystems [e.g. 1, 3, 5–7]. For instance, a study of samples from hot springs [5] found that differences between populations of archaea were mainly due to the geographical distance between sites, rather than to environmental factors. Likewise, a study of freshwater lakes in the US [7] concluded that physical proximity (and thus the intensity of species exchanges among lakes) has an influence on community composition independent of other environmental variables. But even when habitats lie very close together, differences can be seen in the composition of microbial communities which can scarcely be attributed to environmental factors. For example, Eawag researchers characterized the diversity of bacterial communities in various habitats along the shore of a freshwater lake [8]. It was shown that the marsh habitats studied (lake water, epiphytic biofilms, plant litter and sediment) represent distinct microhabitats, but also that bacterial communities in the same habitat types at sites just a few metres apart sometimes differ markedly from each other.

There is now a good deal of evidence to suggest that the capacity of microbes for dispersal is not, as would be assumed by Baas Becking, unlimited, but varies widely from one species to another, depending on the species' ability to survive during transport, to form resistant resting structures (spores or cysts), to reproduce at the new site, etc. On the other hand, we now know that, by evolution, microbes can adapt very rapidly to their environment. While this is not necessarily equivalent to the development of new species, it does require genetic variability within a species. It is thus reasonable to suppose that in addition to cosmopolitan species there are also microbial species with a more local (i.e. endemic) distribution, and that, depending on the particular habitat, microbial communities will develop with different proportions of global and local species.

Worthy of protection – but do we need to? In summary, microorganisms can be said to be both highly diverse and highly significant in terms of the functions they serve. In addition, diversity is frequently considered to be associated with the stability of systems and processes (cf. the article by Eberhard Morgenroth on p. 15). For this reason, microbial diversity in itself – whether or not we regard microorganisms as cosmopolitan – deserves to be protected. But does it also *need* to be protected?

This depends to a large extent on the existence of endemic species. In a new project, using a new method (massively parallel sequencing, see Fig. 2), we therefore intend to address this question, investigating microbial community composition in 30 Swiss lakes. With this high-resolution data set, it will be possible to test the dispersal limitation hypothesis statistically. If it is confirmed that endemic species play a role in natural systems more frequently than has been assumed to date, it would have to be concluded that microorganisms, like other organisms, represent part of the unique biodiversity of a local ecosystem and thus need to be protected. This applies especially in the case of habitats with extreme conditions.

At the same time, microbes highlight certain limits: given their immense diversity, "species protection" for microorganisms, as traditionally understood – with the possible exception of extreme habitats – is neither advisable nor feasible at present. Nonetheless, we should be aware that we lack a systematic understanding of which bacterial communities arise in response to specific environmental conditions and, above all, what consequences this has for key biogeochemical and ecological processes – and ultimately for ecosystems. Accordingly, microbial diversity needs to receive more attention among researchers and policymakers as a fundamental element of biological diversity and ecosystem functioning. ○○○

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Functional diversity in wastewater treatment

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Co-authors: Helmut Buergmann, Kai Udert

Variations in influent loads pose major challenges for biological wastewater treatment. Could increased biodiversity allow for more stable operation, and does this mean that biodiversity should also be protected in wastewater treatment plants? Using molecular biological methods, we can now quantify biodiversity and specific groups of microorganisms in complex systems.

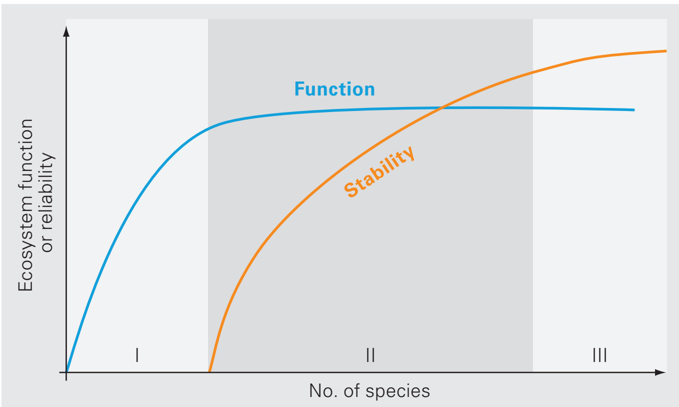
In biological wastewater treatment, biodiversity is deliberately restricted. Operating conditions in biological treatment (e. g., substrate availability, oxygen, residence times) are selected in such a way that desired bacteria accumulate and unwanted bacteria are washed out of the system. The microbial community always comprises an undefined and open culture, which is continuously mixed with new organisms from the influent. The desired bacteria perform specific functions (oxidation of organic matter and ammonium, denitrification of nitrate, removal of phosphorus), and at the same time they should not disrupt the operation of the system – in activated sludge reactors, for example, they must form flocs that settle well in secondary sedimentation.

Operating conditions in biological wastewater treatment plants have generally been developed empirically, on the basis of around 100 years' experience with conventional activated sludge and biofilm processes. Only over the past few decades this empirical approach has increasingly been supplemented by a mechanistic understanding of the growth rates and physiology of the organisms concerned. Effective methods for identifying and quantifying specific groups of bacteria have been available for about 20 years (see the article by Helmut Buergmann on p. 12); to date, however, this information on community structure has had a very limited influence on the design and operation of wastewater treatment plants. Below, the dynamics of biodiversity are illustrated by a number of examples.

Consistent performance despite dynamic changes in microbial communities. Experience from the operation of treatment plants has shown that system performance is reproducible and consistent under constant operating conditions. But what about biodiversity under constant operating conditions? Kaewpipat and Grady [1] operated two laboratory-scale reactors in parallel, under identical and constant conditions. They demonstrated that performance, activated sludge volume and settling properties were largely identical in the two systems during the 6-month operating period. This did not apply to the bacterial community composition, which was analysed by denaturing-gradient gel electrophoresis (DGGE). Despite constant operating conditions, continuous changes were observed in the bacterial communities. While the populations developed in a similar manner for the first 2 months, community composition showed completely different dynamics in the two systems over the next 4 months. From this it can be concluded that community composition and biodiversity in biological wastewater treatment plants will develop dynamically and not necessarily predictably, as a function of the operating conditions.

The greater the functional diversity, the more stable the anaerobic digestion. Fernandez et al. [2] investigated the influence of biodiversity in eight parallel anaerobic reactors. Two inocula differing in bacterial community structure were each used to inoculate four of the eight reactors. During the start-up phase, operating conditions in the reactors were identical, but in the course of the experiment, two sets of communities with different levels of diversity developed in the two groups of reactors,

Fig. 1: Schematic view of the relationship between biodiversity, functional diversity and system stability. As the number of species rises, functional diversity also increases and the species present have mutually complementary effects (Region I). If the number of species is further increased, no new functions appear, but the now redundant species may increase the stability of the system under dynamic conditions (Region II). Still greater biodiversity (Region III) does not lead to any further rise in stability [7].



depending on the inoculum used. When the influent substrate concentration was abruptly increased after the start-up phase, the researchers found that community structure in the reactors with greater diversity was less variable than in the comparison group. Interestingly, however, operation was more stable in the reactors with the less diverse communities (lower accumulation of organic acids). Thus, a straightforward relationship between biodiversity and stability, such as can be posited on the basis of general theoretical considerations (Fig. 1), is not applicable for this microbial system. Fernandez et al. did, however, show that it is functional diversity, rather than general biodiversity, which is associated with system flexibility. In current Eawag projects, efforts are therefore being made to analyse not only the overall community structure, but in particular also the abundance and diversity of those functional microbial groups which are essential for the wastewater treatment process (see Box).

Exploiting habitat diversity in biofilms. The functioning of the wastewater treatment plant "ecosystem" depends not only on biodiversity and functional diversity, but also on the diversity of habitats [3]. Consider this example: in an activated sludge reactor where bacteria grow in small flocs and where there is only one fully mixed tank, all the bacteria are always exposed to the same environmental conditions (assuming that mass transport limitations can be neglected). In contrast, biofilms are heterogeneous systems. Growth conditions in the biofilm are determined partly by substrate availability (Fig. 2A), but also by the local residence times of bacteria in the biofilm (Fig. 2B) [4]. With stable operation, growth and detachment processes are in equilibrium, although the precise mechanisms of detachment processes – and their influence on biofilm structure – have yet to be elucidated [5]. But, in general, it can be said that bacteria growing close to the biofilm surface are removed more rapidly from the system than those close to the substratum. This gives rise to a distribution of residence times – which could also be termed "local sludge age" – across the thickness of the biofilm (Fig. 2B).

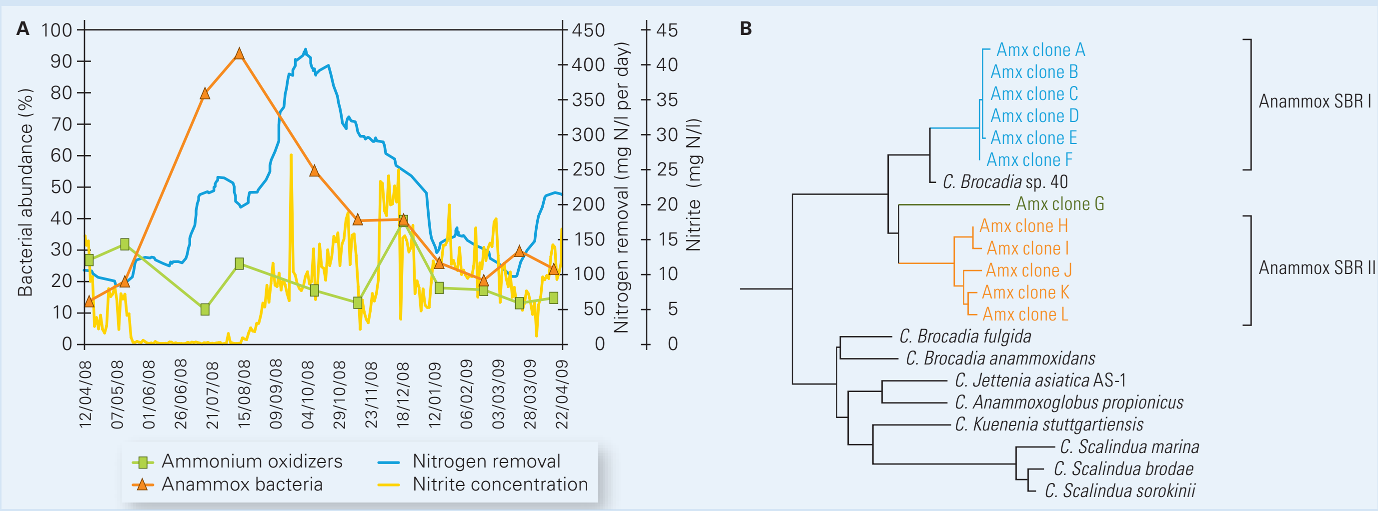
Mass transport limitations are primarily a disadvantage of biofilm processes, as they limit substrate removal n the reactor. How-

Low flexibility associated with low diversity: the example of the anammox reactor

At Eawag, urine source separation and treatment has been extensively investigated as an alternative strategy for wastewater management. In one of these projects, we studied the biological removal of nitrogen with activated sludge flocs in a laboratory-scale reactor. Part of the ammonium is oxidized to nitrite by aerobic nitrifiers. This nitrite is then used by anaerobic ammonium oxidizers (anammox bacteria) to oxidize the remaining ammonium to molecular nitrogen (see also Fig. 3). Among the questions of interest to us is how the bacterial community develops during this process. The reactor had been inoculated with an undefined culture from a wastewater treatment plant, and after the start-up phase we detected various anammox clones of types SBR I and SBR II, which however scarcely differed genetically within their respective groups (Fig. 4B). In the course of operation, the SBR I group became dominant: the anammox bacteria in the reactor thus showed very limited diversity.

In the example shown, a change in the operating parameters (including adjustment of the pH range) from August 2008 led to an unfavourable development of the anammox community. With a certain time lag, there was an accumulation of nitrite and a drop in the performance of the reactor (Fig. 4A). From then on, far fewer anammox bacteria were to be found in the reactor. It remains to be investigated whether the low diversity of the anammox bacteria contributed to the operational problems.

Fig. 4: (A) The greater the proportion of anammox bacteria in the reactor, the higher the nitrogen degradation rate and the lower the nitrite concentration. (B) Phylogenetic tree of anammox bacteria: clones marked in colour were detected in the reactor; all the other anammox bacteria are listed as reference species (Buergmann/Udert/Jenni, in preparation). SBR = sequencing batch reactor.



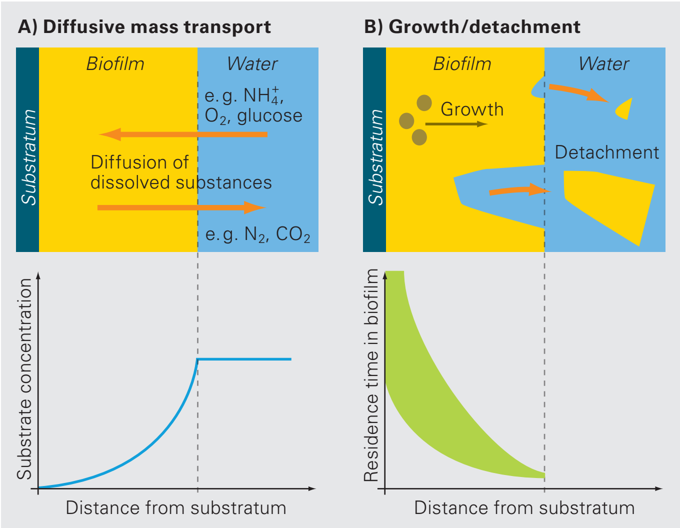
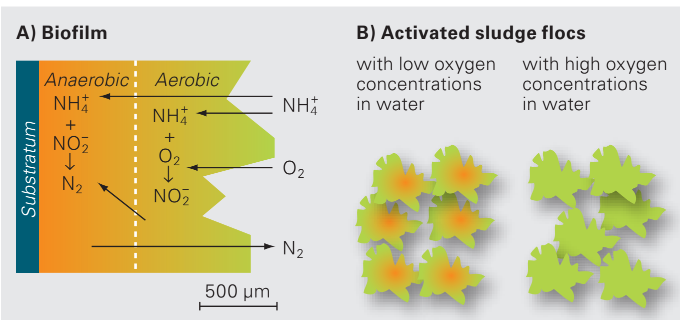


Fig. 2: Growth conditions in the biofilm depend on mass transport (A) and on the local residence time within the biofilm (B) [4, 6].

ever, mass transport limitations can also be deliberately exploited, opening up new opportunities – not only in biofilm processes but also in reactors with activated sludge flocs (Fig. 3). For example, if oxygen is only available at the surface of the biofilm or flocs, zones with different redox conditions will develop on the inside. Aerobic processes will take place in the outer zone (e.g. oxidation of ammonium with oxygen to nitrite) and processes which can only occur in the absence of oxygen will take place close to the substratum of the biofilm or at the centre of the activated sludge flocs (e.g. anaerobic oxidation of ammonium with nitrite = anammox) (Fig. 3). Deliberate exploitation of mass transport limitations thus allows simultaneous aerobic and anaerobic ammonium oxidation processes in the same reactor (cf. Box). As a rule, such reactors are more robust and easier to operate than two separate reactors for the oxidation of ammonium to nitrite and anaerobic ammonium oxidation.

Fig. 3: Simultaneous ammonium oxidation and anammox in a biofilm reactor (A) and in activated sludge flocs with low oxygen concentrations (B). Aerobic: conversion of ammonium with oxygen to nitrite; Anaerobic (or anoxic): conversion of ammonium with nitrite to molecular nitrogen (= anammox). The colouring indicates oxygen availability in the biofilm or in the activated sludge flocs (green: oxygen available, orange: no oxygen available).



The combination of local substrate availability and local residence time thus gives rise to different growth and reaction conditions at the surface of and deep within the biofilm or activated sludge flocs. But we do not yet know nearly enough about the potential offered by these different ecological habitats for wastewater treatment.

Better understanding of functional and habitat diversity. Biological wastewater treatment involves skilful manipulation of the microorganisms in the system so that suitable organisms are selected to carry out the desired processes. In itself, increased bacterial diversity does not necessarily lead to increased performance or stability in wastewater treatment plants. These plants are complex ecosystems, and there is a need for a better understanding both of functional diversity and of the diversity of habitats arising in the biofilm – and how they relate to species diversity. These are fascinating challenges for current research. ○ ○ ○

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The rise and fall of species diversity

The preservation of biodiversity requires a dynamic equilibrium in which speciation occurs just as often as species extinction. But conservation efforts frequently ignore the need to maintain not only the existing diversity of species but also the variety of speciation processes.

Current rates of species extinction are around 100 to 1000 times higher than the average rates in the history of Life on Earth and are comparable to those seen during the five largest mass extinction events in Earth's history [1]. Recent predictions suggest that, if the trend is not inversed, half of all the remaining species will be extinct by 2100. At the same time, fewer and fewer new species will be formed. Despite only a minority of the public being aware of this at present, it is foreseeable that, in the coming decades, the biodiversity debate will exceed the current climate change debate in intensity and urgency.

Speciation can be fast. Two very different interest groups are particularly concerned with changes in biodiversity – conservation ecologists and environmental organizations on the one hand, and evolutionary ecologists on the other. With the exception of a handful of visionaries on both sides, exchange between these two groups is very little. In fact, this is understandable, given the widespread assumption that the timescales relevant for ecological and evolutionary processes are completely different. In reality, however, evolutionary changes occur continuously and are particularly rapid when environments change. Populations react to changes in their environment by undergoing genetic adaptation through natural selection. Adaptation of different populations to different conditions may lead to the formation of new species. This process, known as ecological speciation, can operate within a short space of time, i. e. over a period of decades – even in the case of organisms with relatively long generation times, such as fish and birds. For example, salmon populations that adapted to different spawning habitats have developed partial *reproductive isolation* [1] within 14 generations. In other words, very little interbreeding occurs between salmon adapted to different spawning habitats. Among bird populations which migrate to different wintering areas, reproductive isolation can evolve within 10–20 generations, even though they use the same breeding area. A large sculpin population which resulted from hybridization between two species colonized a new ecological niche in the Rhine River and became isolated from the ancestral species within 20–200 generations [2]. To take a Swiss example, sticklebacks – which until 140 years ago were only found in Basel north of the Jura – have since colonized large areas of the Central Plateau, and there is evidence that they have begun to diversify into a number of different incipient species within this short period of time (Fig. 1).

Fig. 1: The three-spined stickleback – an example of new diversity arising locally over a period of a few decades. Left: a larger form with red breeding coloration, which breeds in the littoral zone of a small lake and is similar to sticklebacks in the surrounding waters. Right: a smaller, endemic form with yellowish-orange breeding coloration, which inhabits the sediment in the pelagic zone of the same lake. Our genetic data suggest that the yellow form arose locally from the red form within the last 50 years.

Simultaneous decrease in speciation and increase in extinction rates. *Evolutionary processes* can, on the other hand, also lead to the extinction of species – even more rapidly than *demographic processes* alone. Classical conservation biology is concerned with extinction caused by demographic processes, which influence population size. But extinction may also be a result of evolutionary processes – even independently of demographic processes. This occurs, for example, when changes in environ-

[1] Terms given in italics are defined in the Glossary.

mental conditions eliminate the relevance of adaptations, thereby removing ecological reproductive isolation between species. As long as there is no environment-independent *genetic incompatibility* between species, they will then merge into a single hybrid swarm. Environment-independent incompatibility usually only develops over a period of several million years. But many species are much younger: more than 40 % of all fish and more than 20 % of all mammalian species fall into this category [3].

While species and species diversity are often treated like static properties in classical conservation biology, evolutionary ecology shows that diversity can only be maintained if a dynamic equilibrium is retained. Demographic and evolutionary processes are both important, and speciation and extinction rates need to be balanced. As is soon apparent to those who study these issues, both processes and both rates are influenced by the same environmental factors. These are precisely the factors which are currently changing at a dizzying pace, namely the physical extent and ecological diversity of habitats. The rapidly progressing loss of habitat and the equally rapid ecological homogenization of habitats are leading inevitably to an increase in rates of extinction due to both demographic and evolutionary processes. At the same time, however, both changes are also leading to a sharp decline in speciation potential. As habitat size decreases, not only population size but also genetic diversity and the efficiency of natural selection decrease. A decline in habitat heterogeneity is associated with a decline in the heterogeneity of natural selection and a reduced potential for the formation of new species by adaptation. The simultaneous decrease in speciation rates and increase in extinction rates leads to a catastrophic biodiversity debt (Fig. 2) [4].

For many years, our research group has been investigating human influences on the processes of speciation and species persistence. As model systems, we use particularly species-rich waters with high rates of speciation and extinction of fish, such as the Great Lakes of East Africa and lakes and rivers in Switzerland. Whether African cichlids or Swiss whitefish, we observe time and again that ecological speciation and extinction are influenced by the same factors.

Collapse of African cichlid diversity. The cichlids of East Africa's Great Lakes are a classical textbook example of speciation [5]. More than 1000 species are endemic to (i. e. found exclusively in) Lakes Victoria (~ 500), Malawi (~ 500), Tanganyika (~ 200), Edward (~ 60) and Mweru (~ 30). These species evolved within the lakes by many events of ecological speciation in short succession, known as *adaptive radiation*. Speciation occurred at a rapid pace. For example, 500 species evolved in Lake Victoria over the past 15,000 years – an average of one new species every 30 years. This was made possible by ecologically heterogeneous habitats and historically large population sizes. Although the total cichlid population of Lake Victoria is split up into more than 500 different species, each individual species shows considerable genetic variation, indicating that large populations existed over long periods, with occasional exchange of genes between species. Large standing genetic variation is a prerequisite for rapid speciation

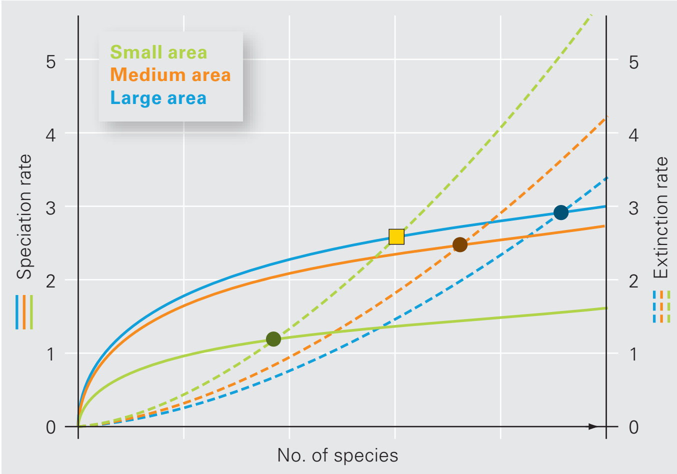


Fig. 2: Dynamics of species diversity in three provinces of different area size. The coloured curves represent speciation and extinction rates in small, medium-sized and large provinces as a function of species diversity. The equilibrium species diversity – where speciation and extinction rates are balanced – is given by the intersection of the respective speciation and extinction curves. In order to predict the influence of a loss of area on species diversity, both speciation and extinction need to be taken into account, as the following example illustrates. Starting from steady-state diversity in a large range (intersection of the blue curves), the new steady-state after a loss of range size – under the erroneous assumption that the speciation rate is unchanged as range size decreases – would be marked by the yellow square. However, as the speciation rate also decreases with range size, the new steady-state is actually established at a much lower level of diversity – namely, at the point where the two green curves intersect (modified from [4]).

Glossary

Adaptive radiation: evolution of several new species from a common ancestor by adaptation to different ecological niches associated with the development of ecological reproductive isolation.

Demographic process: development of population size through changes in birth and death rates under the influence of ecological factors.

Evolutionary process: changes in the genetic composition of populations from one generation to the next.

Genetic incompatibility: possession by potential mates of different gene variants, the combination of which produces offspring whose viability or fertility is reduced, irrespective of environmental factors.

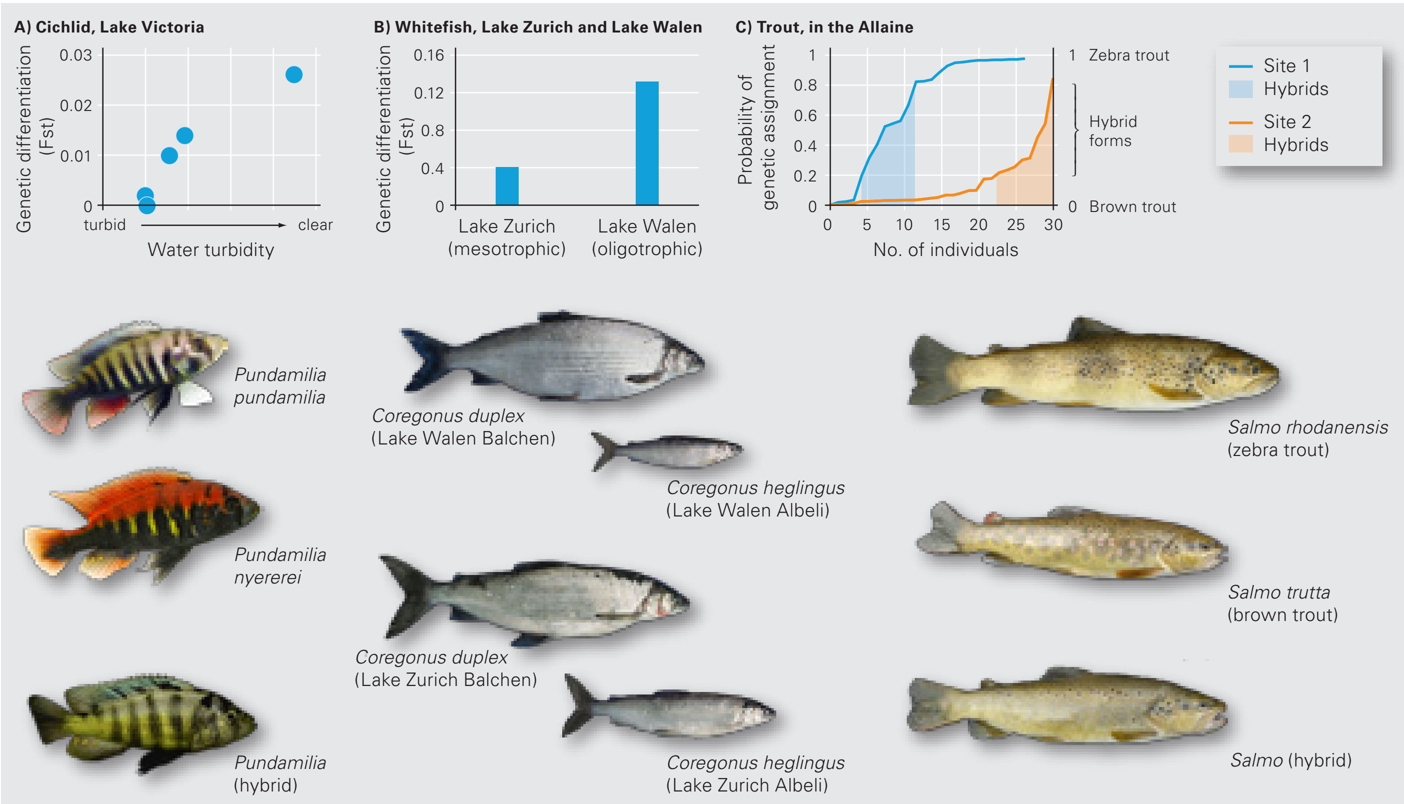
Reproductive isolation: populations are reproductively isolated if the viability or fertility of hybrids is reduced compared with non-hybrids. This may be due to ecological (i. e. environmentally determined) incompatibility or to intrinsic genetic incompatibility.

driven by natural selection for adaptation to different ecological niches. A dominant role in this process can be attributed to water depth gradients, since speciation is often associated with adaptation to light and food conditions at different water depths [6].

However, Lake Victoria is also the site of the greatest mass extinction ever to have been witnessed by scientists. The causes for this mass extinction lie in an interaction between demographic and evolutionary processes. An introduced predator at the top of the food chain, the Nile perch, massively reduced population sizes of many cichlid species in the 1980s. Organic pollution of the lake, which had begun several decades before, led to eutrophication, resulting in widespread loss of ecological habitat diversity. Deeper zones of the lake in particular can no longer support cichlid populations, owing to a lack of light and oxygen. This means that the reproductive isolation of species by divergent selection and adaptation along water depth gradients is weakened or eliminated altogether, and formerly distinct species merge into hybrid swarms (Fig. 3A). Cichlid diversity has literally imploded as a result [7]. The tragedy – from a conservation perspective – is compounded by the fact that, in fish stock management, the various cichlid species are generally lumped together into a single group *(Haplochromis* spp.). Consequently, even though the lake is heavily fished and numerous internationally funded fishery research projects are being carried out, there is no quantitative data either on current or on historical distributions and abundances of the different cichlid species. Some consolation can be drawn from the fact that a large proportion of the species are now included in the IUCN Red List, so their conservation status is at least visible to a wider public.

Alpine lakes: home to the greatest diversity of whitefish species. Switzerland's whitefish have suffered a similar fate. More than 24 different whitefish species are currently known from major Swiss lakes, and several unknown or unrecognized species are likely to exist. Switzerland is thus home to the greatest diversity of whitefish species worldwide, with up to six different

Fig. 3: Three examples of species extinction resulting from the interaction of demographic and evolutionary processes.
A: The genetic differentiation of Lake Victoria cichlids decreases as eutrophication (shown as water turbidity) increases. The species *Pundamilia pundamilia* and *P. nyererei* can now only be detected at sites with relatively clear water. At turbid-water sites, the populations consist of genetically and ecologically undifferentiated hybrids. Each data point represents one site (one island). Fst = Measure used to indicate genetic distance.
B: The whitefish species *Coregonus duplex* and *C. heglingus* in oligotrophic Lake Walen show more marked genetic differentiation than their counterparts in mesotrophic Lake Zurich. In even more eutrophic lakes, only populations of genetically undifferentiated hybrids can now be found.
C: Zebra trout *(Salmo rhodanensis)* and brown trout *(Salmo trutta)* from the Allaine, a tributary of the Doubs. In two stretches just a few kilometres apart, species show quite different levels of genetic differentiation. Thus, at site 1, a few fish are genetically classified as brown trout (values between 0 and 0.2) and a large number as zebra trout (values between 0.8 and 1), while others show intermediate genotypes. At site 2, brown trout and intermediate forms are found almost exclusively. (Photos: A. Hudson, I. Keller, J. Schuler, I. v.d. Sluijs, P. Vonlanthen, O. Seehausen)



species being found in a single lake. Over the past 5 years, we have studied the evolutionary origins of this diversity in detail. It has become clear that, much like in the case of the cichlids, ecological speciation played a key role, and that – here too – this usually occurs along the water depth gradient [8]. In Swiss lakes, just as in Africa, organic pollution and eutrophication have led to a loss of diversity of ecological niches. Several species have merged as a result (Fig. 3B). According to our data, at least a third of the country's whitefish species have disappeared over the past 50 years. This extinction event has gone largely unnoticed in conservation circles. No doubt, this is partly attributable to the fact that the applied literature still gives an oversimplified account of the complex structure of species diversity (just as in the case of the cichlids), and reference is often made in general terms to the whitefish as *Coregonus* spp. [9].

Trout species in Alpine rivers displaced by Rhine trout. Trout are Switzerland's most widely distributed fish. What is less well known is that the country's waters are inhabited by five distinct evolutionary lineages of trout, only one of which is widely distributed in the country. The latter originates from the Rhine catchment. The others come from the catchments of the Danube, Jura Rhône and Po (including the almost extinct marble trout). Over the past 50 years, however, large numbers of Rhine (Atlantic) trout have been introduced as stocked fish in all the other catchment areas. It is well known among scientists and managers that this species displaces indigenous trout in many of these rivers by hybridization and ecological competition. But a largely unknown fact is that the different types of trout, which originated in different ice age refugia, can also differ markedly in their ecologies. Several research groups have found evidence that these trout can coexist as species in some rivers with rather natural habitat structure. In heavily degraded rivers, however, this is not possible; here, the Rhine trout appears to have an advantage and displaces the other species. Although very few refugia remain in Switzerland for the marble trout, the zebra trout (Rhône trout; Fig. 3C) and the other southern types, there is a lack of coordinated conservation efforts. Here too, the explanation may well lie in the fact that these (from an evolutionary perspective) relatively young species are not, or not correctly, recognized in the applied literature – most field guides refer to just one trout, *Salmo trutta* (but see [10]).

Need for cooperation between conservationists, resource managers and evolutionary ecologists. In summary – whether we are dealing with African cichlids, Swiss whitefish or trout – we can see time and again that the loss of biodiversity is driven by changes in both demographic and evolutionary processes, and that speciation and extinction are influenced by the same factors. A successful strategy for the preservation of biodiversity therefore requires an in-depth understanding of both processes and an awareness of the need to maintain not only the existing species diversity but also the variety of processes whereby new species evolve. It is therefore of paramount importance to establish a close dialogue, at the national and international level, between evolutionary ecologists, conservation biologists and resource managers. That to date this happens only to a very limited extent poses serious threats to the protection of biodiversity, not only in the tropics but also in the Alps. In any event, there is not much time left to preserve the endemic diversity of fish species in Switzerland. ○○○

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Invasive species – threats to diversity?

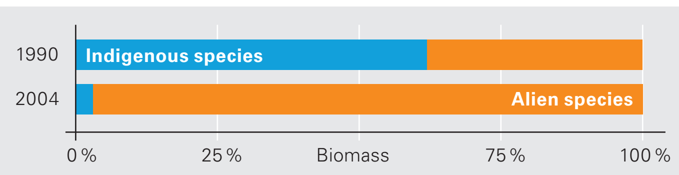
Invasive alien species are a major cause of declines in native biodiversity in both terrestrial and aquatic ecosystems. As well as traditional monitoring programmes, genetic methods are now providing valuable information on new arrivals.

Towards the end of the 19th century, three North American crayfish species were introduced to Europe. The (noble) intention was to boost dwindling crayfish stocks. Since the 1970s, these exotic species have also been observed in Switzerland, where – being more aggressive, resilient and fecund – they have displaced indigenous crayfish species. Unfortunately, the aliens also serve as carriers of the fungus which causes crayfish plague – without suffering from the disease themselves. For indigenous crayfish, however, this fungal infection is rapidly fatal, and Swiss populations have consequently been further decimated.

This example illustrates the threats to biodiversity posed by readily spreading and highly fecund aliens. Invasive species interact with indigenous organisms and, via a cascade of effects, may disrupt the functioning of entire ecosystems. Indigenous species are frequently crowded out or even extirpated as a result (Fig. 1). In this context, inland waters are particularly sensitive ecosystems, for although freshwater only accounts for 0.01 % of the earth's total water volume, it harbours about 12 % of all known species. These include an extraordinarily large number of endemics – i. e. species which are restricted to a particular area. Even so, aquatic organisms have not hitherto been covered by the Swiss biodiversity monitoring programme; lotic benthic macroinvertebrates (all bottom-dwelling creatures of running water) are, however, to be included this year.

Along with ecological impacts, invasive species can also cause socioeconomic damage: this may include reduced yields due to introduced diseases in fisheries and aquaculture, or additional costs for maintenance of infrastructure – e. g. when invasive mussels block water intakes.

Fig. 1: In under 15 years, indigenous invertebrates were almost completely displaced by alien species. An example from the High Rhine [from 6].



In only a few cases does it prove possible for an invasive species to be eliminated and damage limited. For this reason, efforts should focus on preventing new introductions or containing the spread of established species. In order to assess the risks and take appropriate measures, a detailed fundamental knowledge of the invasive organisms' ecology and genetic background is required.

Zebra and quagga mussels: related but different. A particularly notorious invasive species is the zebra mussel *(Dreissena polymorpha).* Originally native to the Ponto-Caspian region (Black, Caspian and Aral Seas), this species was introduced to Central Europe via shipping canals in the late 19th century. From 1960 onwards, the zebra mussel was also found in Swiss waters, where it reproduced and spread rapidly [1]. A single female can produce up to 30,000 planktonic larvae (veligers). In Switzerland, the highest zebra mussel densities – over 1000 individuals/m^2 – were recorded in the 1970s and 1980s. By exploiting this food source, many waterbirds, including the tufted duck *(Aythya fuligula),* were able to extend their wintering areas. Unlike indigenous mussels, which colonize soft sediments, zebra mussels require a hard substrate. Where no such surface is available, they attach themselves to the shells of their native counterparts, with which they also compete for food. Today, zebra mussels are found in a large number of Swiss waters, but each year populations in littoral areas (up to a depth of about 8 m) are decimated by overwintering waterfowl.

A close relative of this species, the quagga mussel *(Dreissena rostriformis bugensis),* is now also spreading: it can already be found in the Rhine at Karlsruhe [2], and it is only a matter of time before it also invades Swiss waters. While the zebra mussel occurs at depths of up to 12–15 m and requires a water temperature of 12 °C to reproduce, the quagga mussel breeds at 5 °C and thrives at depths of up to 120 m. It can therefore be assumed that in these latitudes quagga mussels will be able to reproduce almost all year round. Particularly problematic is the fact that the veligers can settle on intake pipes of municipal water supplies, which lie at a depth of 30–60 m in Lakes Zurich and Constance. Once the juveniles are fully grown, blockages occur, possibly leading to high maintenance costs for the facilities concerned.

Challenges of early detection and identification. Adult zebra mussels can generally be readily distinguished from quagga mussels (see photo), but in the early developmental stages the morphological characteristics are less well marked, which complicates identification. This also applies to other aquatic organisms, especially when juveniles or larval stages are to be identified. But normally these are precisely the stages involved when a species becomes established in a new habitat. Here, genetic markers can be very useful, as they allow organisms to be identified even in the absence of distinctive morphological characteristics.

It is thus already possible to detect species which are suspected of having become established without even laying hands on them or catching them in nets. This is because every organism leaves traces of genetic material. In water samples, genetic material can therefore be isolated from all the organisms present in the waterbody – material which can subsequently be analysed using species-specific gene probes. This method has been used, for example, to track the presence of the invasive American bullfrog *(Rana catesbeiana)* in natural wetlands in France [3].

Stowaways. In the past, natural barriers such as mountain ranges, oceans or continents served as effective boundaries for most species. However, the globalization of trade (with the associated air and sea traffic) and growing individual mobility have led to uncontrolled introductions of alien species (Fig. 2). Species now travel as "stowaways" on commercial goods or are carried inadvertently on tourists' equipment.

But many alien species have also been intentionally introduced to new regions. Long before globalization, numerous useful plants and animals were spread by humans. The species concerned were mainly agricultural or forestry crops or ornamentals, fish (e.g. rainbow trout) and game.

In most cases, aquatic organisms are transported on vessels (e.g. on ships' hulls) or in other water-related equipment (e.g. fishing or water sports gear) or water itself. Among the most important vectors are ballast water (large volumes taken on by unladen vessels to provide stability), inland navigation (particularly through shipping canals such as the Rhine-Main-Danube Canal, which connects the Black Sea region to Central Europe) and aquaculture.

Another factor promoting dispersal in future will be climate change: species may extend or shift their natural range as a result of increased temperatures or altered rainfall regimes.

Quagga (left) and zebra mussels thrive in Central Europe.

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Fig. 2: Introduction routes for the zebra mussel, the Asian clam and the amphipod *Dikerogammarus villosus*.

(Un)avoidable aliens? Not every species arriving in a new habitat (= alien species) is able to establish itself permanently and become invasive. Among vertebrates, the ratio of successful to unsuccessful colonists is one to four. No rule-of-thumb figure is yet available for aquatic alien species.

Many alien species first become locally established, survive for a time as a small population, and then proliferate and spread exponentially. Often, the invaders are only detected during the expansion phase. However, long-term population dynamics are difficult to predict; populations may stabilize at a high level, suffer a permanent collapse after a "boom", or follow a cyclic pattern (Fig. 3). In the Rhine, the zebra mussel population declined sharply following the spread of another invasive species from Eastern Europe – the Caspian mud shrimp *(Chelicorophium curvispinum)* – in 1989. But that was not the end of the story: with the arrival of the amphipod *Dikerogammarus villosus,* populations of the Caspian mud shrimp declined in turn, and zebra mussel densities returned to a high level. A decline in the population of an invasive species may be deceptive, since it will rarely die out by itself.

As it is scarcely possible to eradicate an already established invasive species, measures should be designed primarily to prevent introductions of alien species and also to combat or control isolated populations. This strategy proved successful in the case of the invasive red swamp crayfish *(Procambarus clarkii)*. At the end of the 1990s, two populations of this species in Canton Zurich posed a serious threat to the native noble crayfish. Efforts were therefore made to control the red swamp crayfish by setting traps and releasing native predators. In this way, populations were

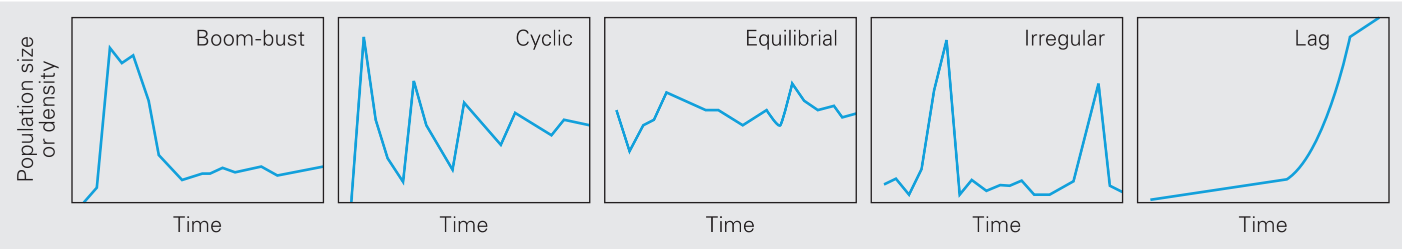

Fig. 3: Five possible long-term trajectories for populations of zebra mussels and other alien species (modified from [7]).

reduced by almost 90 %, thus preventing the further spread of the swamp crayfish and crayfish plague [4].

Key genetic data as indicator of invasion potential. In deciding what measures to adopt, existing damage needs to be taken into account, but it is also important to take preventive action if individual populations have the potential to be detrimental. However, it is not always easy to set priorities. Here, additional decision support can be provided by information on a population's genetic background. The degree of genetic diversity may indicate the population's adaptability or evolutionary potential. Often, a new population will be established by just a few individuals of an alien species. This population will therefore have a limited gene pool. A more worrisome scenario could arise when two genetically distinct lines (e.g. of western and eastern origin) colonize waters and cross-breed. This intermixing means that the alien species can draw on a significantly larger gene pool. If the genetic diversity of the aliens is greater than in the region of origin, there is an increased risk of the new populations becoming invasive.

Need for monitoring of aquatic alien species. In efforts to prevent the spread of alien aquatic organisms, Switzerland could take advantage of its position as a landlocked country. In most cases, species are already established in neighbouring countries and are then introduced via the waterway network. As the possible routes for entry into Swiss waters are limited, they can (or could) be easily monitored. As well as facilitating early detection, close monitoring of waterways would allow regional dispersal routes to be documented. A new species can either spread by natural migration and drift (especially of larval stages) or be introduced indirectly by humans, as for example, the North American amphipod *Crangonyx pseudogracilis.* It was first sighted in the Bay of Bregenz on Lake Constance in 2007 and just a year later was also found in two Swiss lakes – Pfäffikersee and Greifensee [5].

It will scarcely be possible to prevent the proliferation of aquatic alien species in Switzerland altogether. However, regular monitoring measures in rivers and lakes will promote early detection and help to reveal dispersal patterns for individual alien species. Here, genetic methods in particular can provide valuable information.

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Invasive quagga mussel colonization of a propeller in Lake Mead, USA.

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Environmental influences and plankton dynamics

Anthropogenic environmental changes affect natural biodiversity. This can also be seen in lake phyto- and zooplankton, with water fleas *(Daphnia* spp.) reacting particularly sensitively. For this reason, they have been used as model organisms in research.

In 1999, fishermen on Lake Brienz reported a decline of around 90 % in whitefish yields. At the same time, it was observed that the lake was almost completely devoid of *Daphnia* – small crustaceans which are the main food source for whitefish. Eawag studies showed that the lower fish yields were indeed attributable to the disappearance of *Daphnia*. Conditions for the development of *Daphnia* had been extremely poor in the spring of 1999, as the lake water was much colder than usual for the time of year. In addition, a high throughflow caused by heavy rainfall and large volumes of meltwater meant that *Daphnia* were washed away down the Aare. This provides a striking example of the key role played by plankton (see Box) in the food web of lakes.

Most plankters are cosmopolitan

Plankton is the collective term for free-floating aquatic organisms (plankters) which are generally incapable of independent movement and are passively transported by water currents [7]. This group is divided into phyto-, zoo-, bacterio- and myco-plankton (i. e. microscopic plants, animals, bacteria and fungi).

Unlike marine plankton, phytoplankters of the limnetic zone (open lake waters) in particular are cosmopolitan: for example, there is almost no difference between the species found in comparable Northern and Southern temperate lakes, and only a few species and no genera whatsoever occur exclusively in the Northern or Southern hemisphere. Zooplankters, however, have a more marked biogeographical distribution: in general, zooplankton is less species-rich in the Southern than in the Northern hemisphere.

In addition, there is a relatively small number of endemic plankters (only occurring in a specific lake). Thus, in contrast to other groups of organisms, for example, only a few of the plankters observed in Lake Baikal are found exclusively in this waterbody famous for its high level of endemism.

Seasonal variations in plankton composition. In climatic zones with changing seasons, most plankton are periodically confronted with unfavourable environmental conditions – e. g. in the winter, when temperatures fall and little light penetrates. Many plankton species survive such periods thanks to the persistence of a small number of individuals which serve as an inoculum when conditions improve. Other plankters, such as *Daphnia*, form resting stages. This means that lakes also harbour a "hidden" plankton community, comprising seasonally or permanently rare species which can develop into detectable populations under favourable conditions.

With the seasonal growth and disappearance of populations – a phenomenon known as succession – the composition of the plankton community is continuously changing, and different species are dominant according to the season or environmental conditions. Thus, in spring, planktic algae increase and form algal blooms. The phytoplankton then serve as a food source for zooplankton; the more phytoplankton is available, the better the zooplankters develop. When all the phytoplankton has been grazed, the clear-water stage – typical of spring – appears in the lake. Depending on the nutrient content of the water, further algal peaks may arise during the summer.

Plankton succession influenced by various factors. The complex sequence of phyto- and zooplankton growth phases in a lake – and hence also plankton diversity – can be influenced and disrupted by numerous factors. For example, the water temperature in the winter determines the growth rate of the diatom *Asterionella formosa* in the spring [1]. After cold winters, *Asterionella* is able to produce dense algal blooms, whose cells are subsequently attacked by a parasite. With mild winters, however, the parasite is active at a much earlier stage, which means that the growth of *Asterionella* is inhibited and algal blooms are dominated by other, less sensitive species.

In addition, the occurrence of plankton species depends on the trophic status (i. e. nutrient concentrations) of a waterbody. Worldwide, plankton growth is stimulated by the eutrophication of freshwaters. The consequences include turbid water, as well as oxygen depletion following the death of plankton. In this context cyanobacteria (blue-green algae) should be mentioned which profit especially from eutrophication. They produce substances which can be toxic to zooplankton. Scientists assume that such processes will be intensified by global warming [2].

Water fleas: model organisms for environmental changes. As mentioned above, *Daphnia* play an important role in the food web of European lakes. Feeding on phytoplankton and other organic matter, they are themselves a food source for fish. Because *Daphnia* react particularly sensitively to environmental changes, they are used as model organisms in research, e. g. in ecotoxicology tests. In our projects, we are especially interested in how the diversity of *Daphnia* is affected by changes in environmental conditions.

In most Swiss lakes, three *Daphnia* species occur *(D. galeata, D. cucullata* and *D. longispina),* all of which belong to the *D. longispina species* complex which are able to interbreed (hybridize). However, the composition of the *Daphnia* community varies from one lake to another. This is closely linked to the lake's trophic status (Fig. 1). In a study of 43 lakes north and south of the Alps, we found *D. galeata* mainly in eutrophic (nutrient-rich) lakes and *D. longispina* particularly in oligotrophic (nutrient-poor) lakes. Hybrids were found in all the lakes but were most abundant in those which had undergone marked changes in phosphorus loads [3]. In another study, we investigated *Daphnia* resting eggs (ephippia) isolated from sediment cores collected from Greifensee and Lake Constance. In both lakes, only *D. longispina* was found in pre-eutrophication samples (around 1900). As nutrient levels rose, *D. galeata* invaded the lakes and hybridized with *D. longispina* [4]. These hybrids are now abundant in both lakes, dominating the *Daphnia* community in most years.

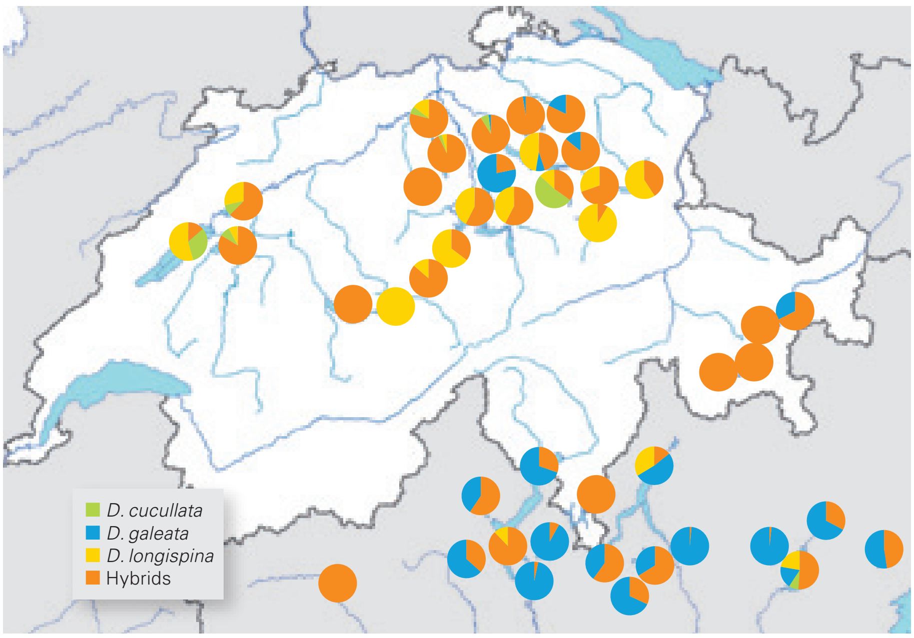
Eutrophic lakes colonized by *D. galeata*. To find out whether it was in fact eutrophication which enabled *D. galeata* to invade lakes such as Greifensee and Lake Constance, we studied the three most oligotrophic large Swiss lakes – Thun, Walen and Brienz [5]. While phosphorus concentrations in these lakes were below 5 µg/l until the end of the 1950s, they rose to as much as 20 – 30 µg/l in the early 1980s. Today, phosphorus concentrations have again stabilized at levels below 5 µg/l. Lake Brienz is the least productive of these lakes, as some of the phosphorus is bound to glacial particles and therefore not available for primary production.

To obtain a more detailed picture of *Daphnia* communities during this period, we analysed ephippia extracted from individual layers of sediment cores. Until the onset of eutrophication, *D. longispina* was the only species found in these three lakes. Interestingly, however, we did not find any *Daphnia* resting stages in sediment layers of Lake Brienz deposited before 1950. This suggests that no *Daphnia* populations were permanently established in this lake before the 1950s. In contrast to Lake Brienz, *D. galeata* became established in Lake Thun and Walen during the eutrophication period. Here, the invasive species hybridized with the native *D. longispina*. Although *D. galeata* later disappeared again, the hybrids remain abundant in both lakes today (Fig. 2). We conclude that anthropogenic changes – even if they are mild, as in the case of Lake Brienz – can have major impacts on plankton composition.

***Daphnia*: extremely adaptable organisms.** Water fleas hatched from resting eggs show remarkable adaptations to the conditions prevailing at the time of deposition. For example, *Daphnia* retrieved from older sediment layers of Greifensee survive longer in high lead concentrations than those from more recent sediments. They were evidently better adapted to the historical conditions, since lead concentrations only decreased as use of this substance declined, with leaded petrol ultimately being banned in 2000 (Fig. 3). Adaptations to different food quantities and qualities could be demonstrated in a similar way [6]: organisms whose parents lived in Lake Constance during the period of maximum eutrophication grew more successfully than others when they received high levels of dietary cyanobacteria (containing phosphorus).

These microevolutionary processes reflect the strong selection pressure exerted by anthropogenic changes on *Daphnia*

Fig. 1: *Daphnia* community composition in 43 lakes north and south of the Alps (modified from [4]).



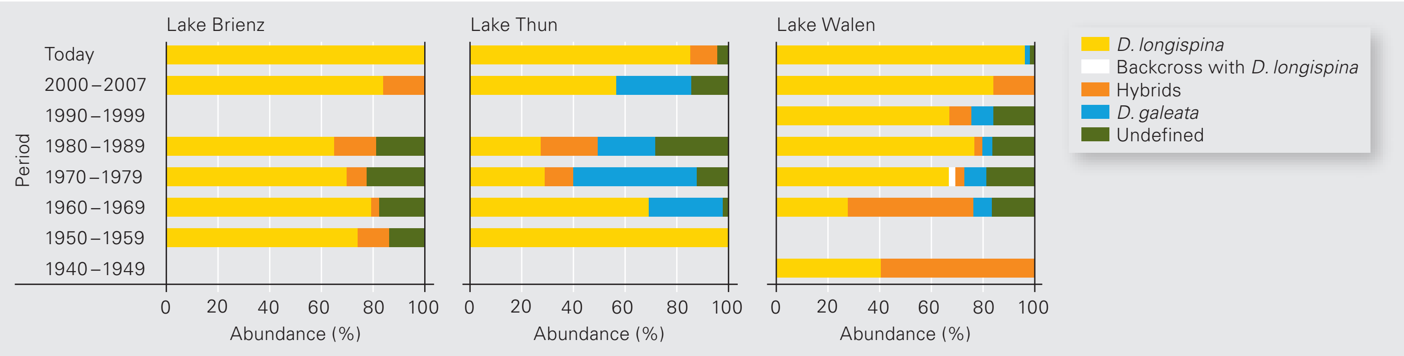


Fig. 2: *Daphnia* community composition in three oligotrophic Swiss lakes since the 1940s.

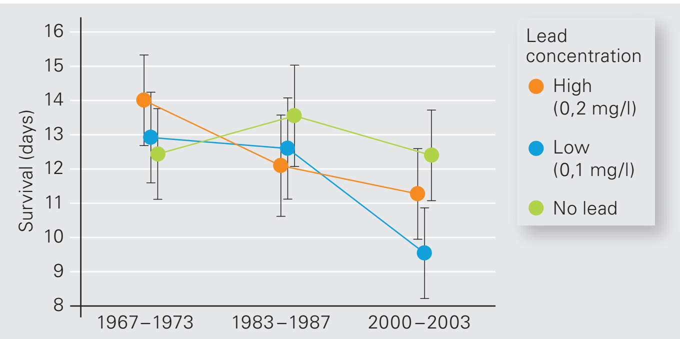
populations. However, these findings also show how flexible *Daphnia* are – because of their ability to survive adverse conditions as a resting stage and also to adopt characteristics of other *Daphnia* species by hybridization. The water flea seems to be able to adapt even to severe changes in its habitat.

Plankton: a vital role in the food web. Overall, our studies of the plankton model organism *Daphnia* show how environmental influences can affect the growth and the composition of the *Daphnia* community – results which, most likely, could be confirmed in a similar way for other plankton species.

In addition, which plankton species – if any – establishes in a lake determines the biotic structure of the ecosystem and ultimately also the diversity of other species. This is illustrated by the above-mentioned example of the massive decline of whitefish in Lake Brienz, which was due to the disappearance of the *Daphnia* population.

Being cosmopolitan, plankton species are generally less at risk, but because they play such a vital role in the food web, it is important to carry out long-term biomonitoring, such as is already performed in Switzerland for some aquatic organisms. In the case of plankton, however, biodiversity protection clearly needs to be addressed at the habitat level. ○ ○ ○

Fig. 3: *Daphnia* hatched from resting eggs from different periods are more tolerant of lead if their parents were accustomed to high lead concentrations in lake water. Leaded petrol was not banned until 2000.



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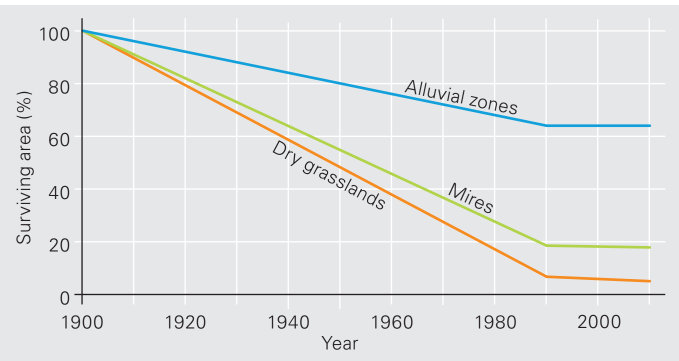
A biodiversity strategy for Switzerland

Biodiversity is a vital resource. The preservation and promotion of biological diversity is therefore a fundamental social duty and an economic necessity. At the national level, the Federal Office for the Environment is currently developing a biodiversity strategy on behalf of the Federal Council.

Ecosystems store carbon dioxide, supply clean drinking water, form and maintain fertile soils, produce goods such as food, timber and fibre, offer protection against avalanches, rockfalls and floods, provide active ingredients for pharmaceutical research, and deliver raw materials for numerous consumer products and technologies. These ecosystem services are a result of the activities of countless organisms – from bacteria through plants to vertebrates – all of which interact to form the complex ecological structure underlying the balance of nature.

The basis of all natural processes is biodiversity. This encompasses the entire genetic information (genome) of organisms; different species of animals, plants, fungi, bacteria, etc.; genetic diversity within species (e.g. subspecies, varieties and breeds); the various ecosystems which are formed and sustained by species (e.g. wetlands, waterbodies, forests); and the interactions occurring within and between these various levels.

Fig. 1: Heavy losses of valuable habitats. Since 1900, there has been a sharp decline in the area of formerly widespread habitats – alluvial zones, mires and dry grasslands. Alluvial zones were mainly affected by river straightening projects; mires were lost to peat-cutting or converted to farmland; dry grasslands were either more intensively managed or were disused and reverted to woodland. The total area lost between 1900 and 2010 is 36 % for alluvial zones, 82 % for mires and 95 % for dry grasslands. But it should also be borne in mind that major changes had already taken place before 1900. In the case of alluvial zones, the area lost between 1850 and the present amounts to 71 % (from [1]).



Preserving ecosystem functioning. Freshwaters also provide numerous important ecosystem services. These include the safe transport of water and sediment, groundwater recharge, moderation of flood peaks and degradation of organic pollutants. Watercourses, criss-crossing the landscape like arteries, make an important contribution to habitat connectivity. In addition, diverse lakes, ponds, rivers and streams are elements which enliven the landscape and are highly attractive for recreation seekers. Moreover, freshwaters harbour innumerable animal and plant species. Worldwide, inland waters cover only 0.3 % of the total land mass but are home to around 12 % of the world's fauna. In Switzerland, 8 % of all animal species and about 4 % of plants (aquatic plants only) are dependent on freshwater habitats.

If freshwaters are to be able to provide their ecosystem services, they must be ecologically functional. Thus, protecting biodiversity means preserving vital resources. Ideally, ecosystem services should not be impaired by any type of use. But in reality, the situation is quite different: over the past two centuries, the area of freshwater habitats has often been severely reduced and they have been heavily modified by a variety of interventions (Fig. 1). These developments are reflected in the Red Lists (Fig. 2). Over 60 % of all aquatic plants are threatened – by far the highest proportion of any ecological group.

According to federal figures extrapolated from cantonal surveys, about a quarter of all watercourses exhibit poor morphological quality, e.g. because the banks or beds have been engineered or the riparian zone is too intensively managed. A considerable proportion of rivers and streams are culverted. Less than half have adequate room, with an appropriate riparian zone.

The quality of our waters is reduced – sometimes substantially – by numerous other factors. For example, inadequate residual flows downstream of hydropower plants reduce the habitat area and alter the flow regime. A new challenge is posed by micropollutants (e.g. endocrine disruptors, biocides, pharmaceuticals, nanotech substances) which can affect biodiversity.

In many places, native species have been completely displaced by invasive alien species. In some river sections, invasive species such as the Asian clam are dominant. Since invasive aliens first appeared in the High Rhine around 1995, a number

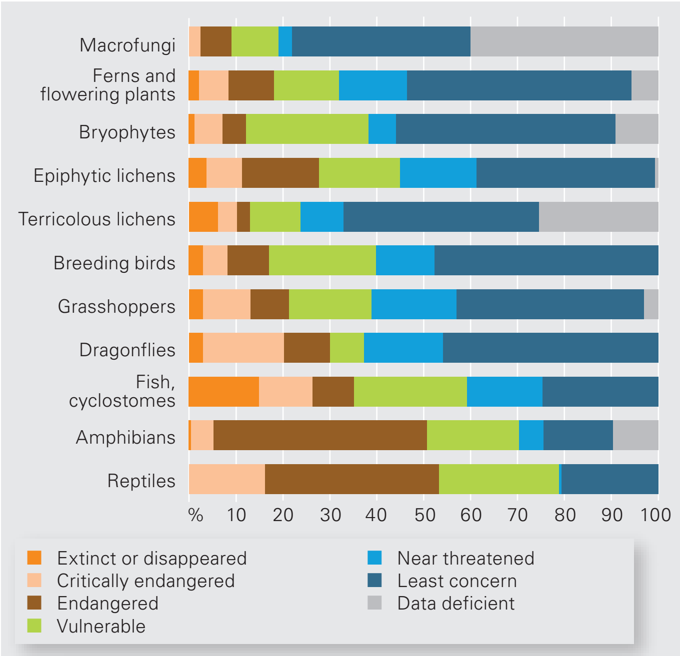


Fig. 2: The number of species included in the Red Lists of Threatened Species in Switzerland varies from group to group. Among the vertebrates, 70 % of amphibians and 79 % of reptiles are threatened. The need for further research is indicated by the proportions of species for which data is deficient [FOEN].

of native species have disappeared or become very rare. Climate change is placing additional pressures on biodiversity. For example, the surface temperature of Lake Zurich has risen by more than 1 °C in the last 40 years, and the water at a depth of 20 m is now about 0.5 °C warmer.

There can scarcely be a more important concern than preserving and promoting vital natural resources and the wide variety of services provided by ecosystems. But this is only possible on the basis of a high level of biodiversity. The various threats to which freshwaters are exposed make it clear that the protection of biodiversity for present and future generations represents a societal, cross-sectoral and international task, for which the state, business and civil society are jointly responsible. The long-term preservation of vital natural resources is also a constitutional requirement under Article 2 Paragraph 4 of the Swiss Federal Constitution.

Developing appropriate instruments. Essentially, Switzerland has a wide range of instruments for promoting sustainable forms of use, controlling landscape interventions, preventing pollution, and preserving habitats and species. However, as has been repeatedly pointed out in performance reviews by scientists, administration officials and the OECD, while existing instruments and measures are good, and in some cases successful, they are by no means adequate. They have not been able to stop the creeping loss of habitats and the species which depend on them, or the deterioration of habitat quality. Clearly, a genuine reversal of these trends cannot be achieved with the available instruments and resources alone (Table). There is a lack of measurable targets and priorities. There are deficiencies both in enforcement and in coordination between the federal, cantonal and municipal levels and between different sectoral policies (e. g. agriculture and water protection). In addition, measures and instruments are lacking for certain areas. At the same time, insufficient priority is accorded to the preservation and promotion of biodiversity in the assessment of competing interests.

As a result, the decline of biodiversity in Switzerland is continuing. It should be recalled that, in 2002, Switzerland and the other Parties to the Biodiversity Convention adopted the target of achieving by 2010 "a significant reduction of the current rate of biodiversity loss at the global, regional and national level". European countries, including Switzerland, went one step further: At the 5th "Environment for Europe" Ministerial Conference, held in Kiev in May 2003, they resolved to "halt the loss of biological diversity at all levels by the year 2010". This objective was not achieved at the national, regional, or global level. The European Union has therefore set a new target: the loss of biodiversity and ecosystem services is to be halted by 2020 and ecosystem services are to be restored as far as possible.

Long-term preservation of biodiversity. In September 2008, the Swiss Parliament voted to include the development of a strategy for the preservation and promotion of biodiversity in the legislative programme for 2007–2011. In January 2009, the development of the Swiss Biodiversity Strategy was commenced under the direction of the Department of the Environment, Transport, Energy and Communications (DETEC). The project is being supported by an expert group with representatives from federal offices, cantons, business and academia and also by interest groups.

Changes in biodiversity associated with the use of waters between 1900 and 2010 (from [1]).

	1900–1990	1991–2010
Habitats		
Rivers and streams	⬇	⇩ ⇨
Lakes	⬇	⇩ ⇨
Temporary waters (pools)	⬇	⇩
Alluvial zones	⬇	⇨
Springs	⬇	⇩
Groups of organisms		
Amphibians	⬇	⇩
Fish	⬇	⇩
Invertebrates	⬇	⇨
Vascular plants	⬇	⇨
Genetic diversity		
Fish	⇩	⇩

⇩ ⇧ Slight increase/decrease in biodiversity
⬆ ⬇ Substantial increase/decrease in biodiversity
⇨ Unchanged biodiversity
Low initial level
High initial level
Intermediate initial level
No data

The invasive Asian clam has also been increasingly spreading in Central Europe since the mid-1980s (see also Fig. 2 on p. 23).

The Biodiversity Strategy focuses on those areas where – in the light of global and national analyses – action is urgently required. In addition, where appropriate, it seeks to flesh out or supplement existing or concurrent political programmes, schemes and action plans. The overarching aims have already been defined by the Federal Council: "Biodiversity is rich and capable of reacting to changes. Biodiversity and the associated ecosystem services are to be preserved over the long term." The achievement of these goals is based on four key elements:

- Biodiversity conservation and promotion areas are designated and subject to binding safeguards.
- Resource use is sustainable.
- Biodiversity is understood by society to be a vital resource and ecosystem services are promoted by economic means and accorded greater weight.
- Switzerland's responsibility for global biodiversity is more fully exercised.

An economic duty. According to environmental economists, a near-natural and diverse ecosystem – with the greatest possible variety of species and genes, adapted to a given habitat – can be compared to a diversified investment portfolio. Each species in an ecosystem reacts differently to changes. If different species are present, the likelihood of ecosystem services being lost – e.g. after a drought – is lower. The more diverse an ecosystem, the greater its resilience – in the sense of an ability to tolerate changes without any loss of the ecosystem's function, structure or services. Particularly with regard to climate change and other environmental changes, the maintenance of resilience – as a form of insurance – is essential. In the future, therefore, greater weight will need to be attached to the precautionary principle than in the past.

Usually, those who cause a loss of biodiversity do not either bear the costs or suffer the consequences. This "market failure" (in the economic sense), which is typical of the environmental sector, is a key factor in the overexploitation or impairment of biodiversity. The Biodiversity Strategy could lead to increased application and further development of the polluter-pays principle with regard to the preservation of ecosystem services.

One important component of the Biodiversity Strategy should be Switzerland's responsibility for global biodiversity. Since the middle of the last century, Switzerland's resource consumption – expressed in terms of its ecological footprint – has risen to four times that which the area of the country would permit. The extraction of raw materials and the production, use, disposal and recycling of these goods have direct or indirect impacts on global biodiversity.

With the Biodiversity Strategy currently in preparation, Switzerland is complying with Article 6 of the Convention on Biological Diversity. Many Parties to the Convention – including a number of developing countries – have already developed and adopted a biodiversity strategy. In its own interests, Switzerland must not stand apart. The range of measures contained in the national strategy should help to ensure that our vital resources or "natural capital" are preserved and promoted over the long term. Specifically, this involves higher-quality habitats and more – appropriately interconnected – biodiversity priority areas. The Biodiversity Strategy is addressed not only to the federal, cantonal and municipal authorities, but to all stakeholders within our society. The strategy can only be successfully implemented if the cause of biodiversity is embraced at all levels and by all sectors. Let us invest jointly in the infrastructure of life! It will be worth it! ○○○

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In brief

NRP 61 success for Eawag

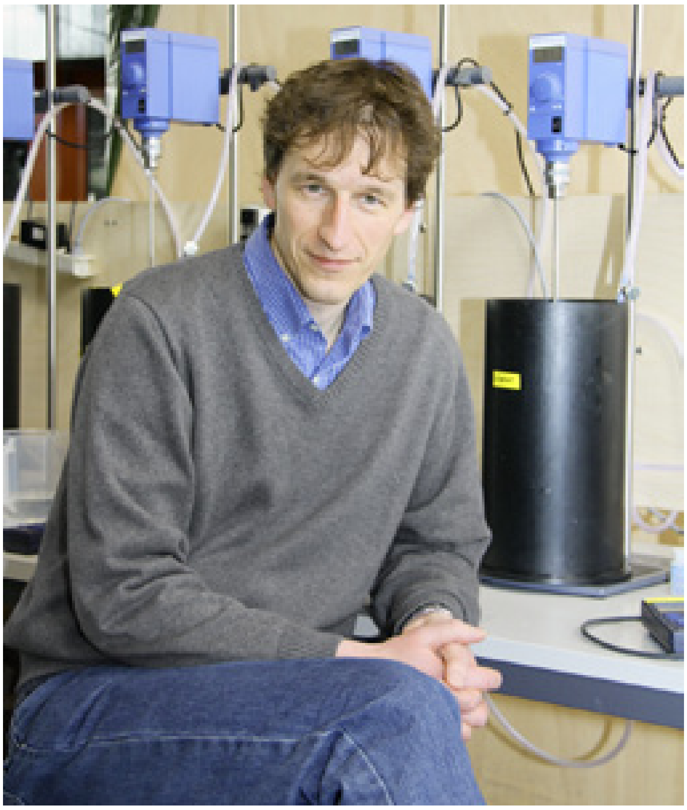
The Swiss National Science Foundation has launched the National Research Programme on "Sustainable water management" (NRP 61). Eawag scientists are participating in 8 – and will be leading 5 – of the 16 projects. At the beginning of March, the participants gathered for a kick-off meeting in Solothurn. The aim of NRP 61 is to develop scientific foundations to help meet future challenges in the water management sector. Climate change and socio economic changes – globally and nationally – are leading to increased competition between different water uses, such as drinking water and hydropower. To prevent shortages and conflicts, there is a need for new global strategies oriented towards near-natural and sustainable resource management. The programme will involve close cooperation between research and practice.

Eawag research post for ETH Professor Eberhard Morgenroth

At the beginning of May, environmental engineer Eberhard Morgenroth, who succeeds Willi Gujer as Professor of Urban Water Management at the ETH Zurich, gave his inaugural lecture. Like his predecessor, Morgenroth will be carrying out research at Eawag and teaching at the ETH. This is precisely what attracted him to his new position. Having taken his Master's in the US and his doctorate in Germany, he gained broad experience in research and teaching at the Technical University of Denmark (Lyngby) and the University of Illinois (Urbana-Champaign). At Eawag, Morgenroth appreciates the combination of numerous disciplines under one roof, the lively exchanges with colleagues and the opportunity to try out even unconventional ideas. For him, another major plus point is Eawag's close links with practitioners: "The creative tension between basic research and practical implementation makes life particularly interesting here!"

Bundesverdienstkreuz for Alexander Zehnder

For outstanding services to German science, former Eawag Director Alexander J.B. Zehnder has been awarded the Order of the Federal Republic of Germany, 1st Class. The decoration was presented by Dr Georg Schütte, State Secretary at the Federal Ministry of Education and Research, on behalf of the German President Horst Köhler on 10 February 2010 in Bonn. Alexander Zehnder is internationally renowned for his work on sustainable development in partnership with business and society, not least in Germany. He served on the Senate of the Helmholtz Association for 13 years and remains an active member of the Bio-economy Research and Technology Council, which supports the development of the bio-economy in Germany. During and since his tenure as Eawag Director, Alexander Zehnder has thus helped to shape and strengthen research within and beyond Switzerland's borders.



In brief

New head of Eawag-Empa library

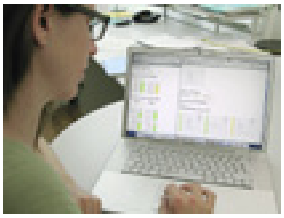
"The modern library reaches users at their workplace," says Lothar Nunnenmacher. Accordingly, the new head of the Eawag-Empa library, who took up his post in April, plans to further expand electronic services for researchers. Nunnenmacher has held senior positions at the libraries of the Institute of Technology and the Charité in Berlin, and from 2006 he was head of collection development at the ETH Zurich library. He is therefore ideally qualified for his first major task in his new role: the Eawag-Empa library is to merge with those of the two other research institutes – WSL and PSI. In addition, despite publishers' price rises, the aim is to continue to provide or even expand the range of media available.

EPFL professorships for two Eawag scientists

At its meeting in May, the ETH Board appointed two Eawag scientists as professor at the EPF Lausanne. Eawag Director Janet Hering (left) was appointed full professor of environmental chemistry at the School of Architecture, Civil and Environmental Engineering. This means that, like her counterparts at Empa (Gian-Luca Bona) and PSI (Joël Mesot), she holds a dual professorship at the ETH Zurich and the EPFL. Kristin Schirmer, head of the Environmental Toxicology department, will now serve as adjunct professor at the EPFL. These appointments underline the existing research cooperation between Eawag and the EPFL and should strengthen ties between the institutions in the ETH Domain.

TransCon2010 conference

Do transformation products of organic contaminants pose a risk to the environment? This question will be addressed at TransCon2010 – a conference being organized by Eawag, which will take place from 12 to 17 September at the Centro Stefano Franscini on Monte Verità in Ascona. The latest research findings from laboratory and field studies and from computer modelling will be presented and discussed at this event. The aim is to develop a common understanding of how to deal with transformation products in chemical risk assessment and environmental monitoring. The conference is designed for researchers and experts from industry and regulatory authorities, and should be of interest to chemists, ecotoxicologists, microbiologists and engineers. www.eawag.ch/transcon2010



Sustainable "Self" module destroyed by fire

At the beginning of April, the "Self" living/working module burnt down. The container-sized unit, set up outside the Zurich Museum of Design, was completely destroyed despite a major fire brigade operation. "Self" was constructed according to state-of-the-art design principles in a joint project involving Empa, Eawag, Zurich University of the Arts (ZHdK) and the University of Applied Sciences Northwestern Switzerland. The aim was to demonstrate that it is possible to live and work comfortably without external energy supplies and with an internal water cycle. The fire is believed to have been caused by a technical defect in the battery system. The damage amounts to several hundred thousand Swiss francs – not including the countless working hours invested in this project by scientists and technicians. Fortunately, a second shell exists, which is now to be fitted out.