Ole Seehausen, evolutionary ecologist, is head of the Fish Ecology and Evolution department and Professor of Aquatic Ecology at Bern University.

# 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

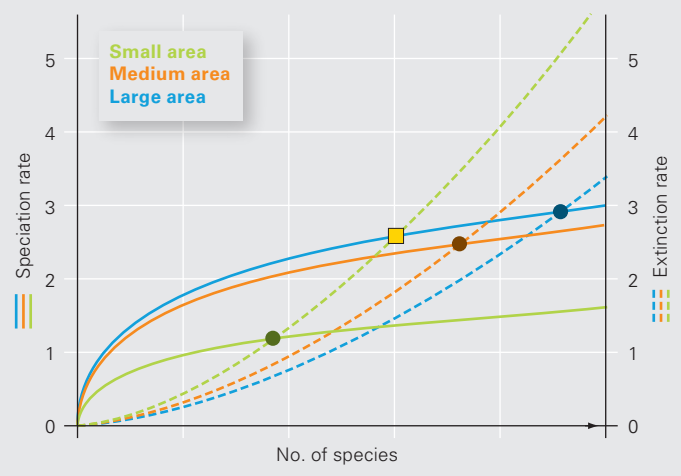



Fig. 2: Dynamics of species diversity in three provinces of different area size. The coloured curves represent speciation and extinction rates in small, medium-sized and large provinces as a function of species diversity. The equilibrium species diversity – where speciation and extinction rates are balanced – 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.

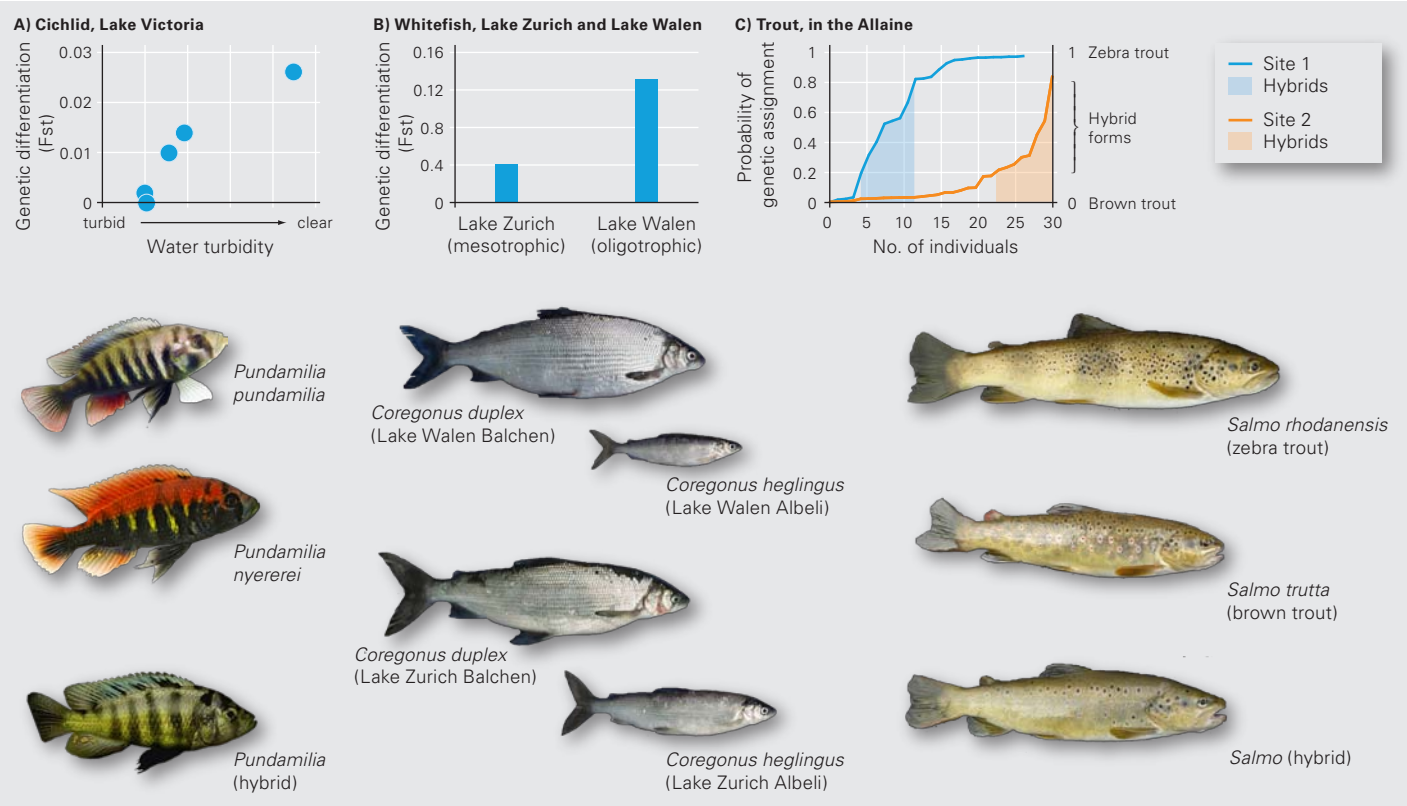
*Reproductive isolation:* populations are reproductively isolated if the viability or fertility of hybrids is reduced compared with non-hybrids. This may be due to ecological (i. e. environmentally determined) incompatibility or to intrinsic genetic incompatibility.

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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