Evolutionary processes: a fundamental element of conservation

The diversity of cichlid fishes in African lakes is influenced by local speciation processes to a much greater extent than was previously supposed. Data from prealpine lakes point in a similar direction. These findings need to be taken into account in efforts to conserve biodiversity. *By Sibylle Hunziker*



Fig. 1: The exceptional diversity of cichlids in African lakes is mainly attributable to local development of new species, rather than to immigration of existing species. Photo: cichlids from Lake Malawi, on display at the Georgia Aquarium (Atlanta, USA).

Lake Mweru, in Central Africa, is home to 43 different species of cichlids – over five times more than Lake Chad, which hosts a mere 8 species despite being almost twice as large (surface area: 9,400 square kilometres). But while 31 of the species in Lake Mweru are endemic – i.e. they arose in situ from a small number of immigrant species and are not found elsewhere – no new species have developed in Lake Chad; it is thus inhabited solely by colonists. Similar contrasts can be observed across the 46 African lakes predominantly inhabited by cichlids, whose species richness was compared by a team of Eawag researchers. In the 23 lakes where speciation has occurred – from the very smallest, with an area of barely a square kilometre,



to Lake Victoria (68,880 square kilometres) – the number of species per square kilometre is up to ten times higher than in lakes of comparable size lacking endemic species.

Evolution: the main driver

These findings are remarkable since, according to the classical island biogeography theory, the species richness of an isolated environment is determined by the relationship between immigration and extinction, and it increases proportionally with surface area; large areas are expected to offer more ecological niches than small ones.

For more than 1200 cichlid species from 46 African lakes, species-area relationships have now been studied in detail by Catherine Wagner, Luke Harmon and Ole Seehausen of Eawag and the Universities of Idaho and Bern, using information obtained from the literature, database records and their own research. In the light of earlier findings, not only lake area but also depth and energy (solar radiation) were included in the analysis. A comparison involving various statistical models confirmed that the limits to diversity are influenced by all three environmental factors – particularly by depth, since deep lakes provide the most favourable conditions for a variety of ecological niches.

Evolutionary factors were shown to have an unexpectedly marked influence on diversity. In all cases, species richness is orders of magnitude higher when community assembly results from the development of new species rather than purely from dispersal. In other words, the eco-

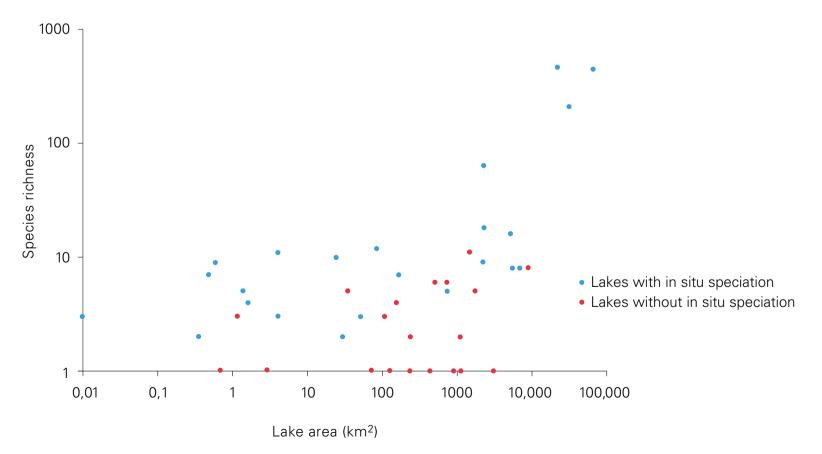


Fig. 2: For lakes with in situ speciation (blue dots) larger than 1000 square kilometres, the species-area curve shows an exponential increase, compared with a linear increase for lakes in whitch diversity is based purely on immigration (red dots).



logical limits to diversification are raised dramatically by in situ speciation. The difference increases with lake area: from a little over 1000 square kilometres upwards, species richness in lakes with speciation increases exponentially, whereas in lakes without speciation the increase remains linear (Fig. 2). Thus, Lake Malawi, with an area of 22,490 square kilometres, is just over twice as large as Lake Chad, but the number of different cichlid species found there is 57 times higher. Of these species only 7 are immigrants, while the remaining 453 are endemic – i.e. they evolved locally from some of the original colonists.

The researchers suggest that the exponential increase in endemic species within very large lakes is due to interactions between various speciation processes and various coexistence mechanisms. In lakes of this size, similar speciation processes may occur at several sites simultaneously, thus additionally giving rise to regional endemism within a single lake. At the same time, ecological niches are probably more tightly packed for the numerous cichlid species developing in situ than for small numbers of colonists, as many new species arise through adaptation to different subsets or combinations of available resources and niches – including the species already present.

No evidence was found that lake size determines whether or not speciation can occur. Rather, in an earlier study, the researchers concluded that ecological opportunity (habitat diversity) and sexual selection (mate choice) are key factors in the diversification of cichlid species.

Interactions between environmental changes and evolution

These investigations show that diversity is indeed influenced by the dispersal of species and by environmental factors such as lake area, as posited by the ecological island theory. However, they also indicate that the development of species richness is significantly influenced by local speciation processes, which follow their own logic and are not reducible to ecology. The study thus dem-onstrates that evolution shapes the way in which ecosystems develop, their dynamics and their functioning. As Catherine Wagner notes, "Our findings contribute to a better understanding of the causes of biodiversity, and they also confirm that the habitats of endemic species deserve particular attention in practical conservation efforts."





Fig. 3: Speciation processes comparable to those in Africa may have contributed to the diversity of whitefish in Swiss lakes.

Stefan Kubl

Using modern methods of genetic analysis, the scientists now plan to elucidate the origins and diversity of fish in Swiss lakes (Fig. 3). Candidates for species density rivalling that of the cichlids are the whitefish and char. Ole Seehausen comments: "The analysis being carried out as part of 'Projet Lac' – our systematic inventory of fish populations – is expected to produce interesting findings for those lakes which never lost their endemic species as a result of pollution." But irrespective of this, he adds, the findings from the African lakes provide another strong argument for explicitly recognizing that the maintenance of evolutionary processes is fundamental to conservation: "As indicators of biodiversity, they are just as important as diversity at the genetic, species and ecosystem level."

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