# Ecological isolation despite physical connectedness: evolution-dependent species richness in large and deep lakes

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The relationship between species richness and ecosystem size remains incompletely characterized for lakes. Some of the large lakes of the world have a long history of investigation as hotspots of endemic species diversity, but other large lakes are very poor in species, and the richness of the former is confined to a handful of taxa. I will try to reconcile these observations, specifically working with fish communities.

We have studied the relationship between richness, physical properties of lakes and species traits for assemblages of cichlid fish across more than 40 African lakes. In this data set we observed that lake surface area and lake depth best predicted species richness. Surprisingly, lake age had no effect at all. When we partitioned species diversity into a component that was locally evolved and an immigration component, it emerged that the process of intralacustrine speciation increased the slope of the species-area relationship from $z = 0.132$ to $z = 0.250$ leading to more species per area by an order of magnitude (Wagner et al. 2014). From these observations one may conclude that assembly by immigration alone is insufficient to generate saturated lacustrine communities, and that species richness is additionally constrained by lack of speciation within lakes. In the same data set we observed that the depth of lakes and the presence of species traits that facilitate speciation were strong predictors of whether speciation happens. Speciation requires deep lakes and rapidly evolving mating systems (Wagner et al. 2012). When both are given and cichlids radiate, they diversify into successively greater water depth with successive speciation events and they eventually fill the entire oxygenated habitat of the lake (Seehausen 2015). When cichlids do not radiate, they remain confined to a limited sector of the lake, mostly shallow littoral habitat. Contrary to common thinking, cichlids did not require isolated lakes to radiate. Up to 50 other fish species have colonized the larger of the African Great lakes, but with a few exceptions, all of them remained confined to shallow littoral habitats and only very few speciated within the lakes. The bulk of the fish biomass in deep and offshore waters are most often cichlid fish.

More recently we started uncovering similar speciation patterns and species-area relationships for fish in the archipelago of European pre- and subalpine lakes. Several lineages of salmonid fish have made intralacustrine radiations, and these radiations can fill the major physical habitats of the lakes, but where they did not radiate (or their radiation was lost due to anthropogenic impact), their single populations tend to be confined to shallow sectors of the lakes (Vonlanthen et al. 2012). Like in African lakes, many other fish species have colonized these lakes too, 30 or more in the larger lakes. Yet, very few are able to colonize deep water and pelagic habitat.

Lakes are often likened to oceanic islands as being physically isolated from rich “continental” species pools. However, the more appropriate concept for lakes may be one of ecological isolation rather than physical isolation. Lakes that harbour large endemic radiations tend to be well-connected to river networks and harbour a rich diversity of non-endemic fish that colonized from the rivers. However, most of these lack the adaptations required for survival and reproduction in profundal and pelagic lacustrine habitats. Hence, the resources in these habitats are accessible only to a very small subset of the colonizing species. For fish to utilize the richness of lacustrine resources, endemic diversity has to evolve in every case from these colonists through the process of adaptive radiation.

I will discuss questions that emerge from this set of observations. Specifically, on the evolutionary side, I will discuss the role of ecological versus physical and biotic isolation among lake faunas and the "transporter hypothesis" for gene transfer between lakes to predict likelihood and rate of adaptive radiation. On the ecosystem side I will discuss expectations for effects of intralacustrine radiations on the biodiversity – ecosystem function relationship. Time permitting, I will end with notes on the problem of the shifting baseline syndrome in understanding changes in the fishery of heavily managed European lakes.

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