

Ecology and Evolution of the African Great Lakes and Their Faunas

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Annu. Rev. Ecol. Evol. Syst. 2014. 45:519–45

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

This article's doi:
10.1146/annurev-ecolsys-120213-091804

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Keywords

African Rift, species flock, adaptive radiation, speciation, morphological evolution, ecosystem functioning, biodiversity conservation

Abstract

The Great Lakes of East Africa are collectively the earth's most remarkable and species-rich freshwater feature. Intrinsic biological factors and extrinsic ecological opportunities allowed much of the lakes' spectacular biological diversity to evolve through evolutionary (often adaptive) radiation and explosive speciation. Beyond evolutionary patterns and processes that led to this remarkable biodiversity and its astonishing morphological disparity, we highlight ecosystem functioning and complex biotic interactions such as coevolution. Comparative biogeographic patterns for vertebrates and invertebrates are discussed, as are patterns of diversity and disparity through the late Cenozoic. We demonstrate that the African Great Lakes, because of excellent fossil archives, are a phenomenal setting to integrate micro- and macroevolution. Unfortunately, these amazing ecosystems are also subject to various anthropogenic stressors at global and regional scales, which have already impacted their stability and threaten part of their extraordinary biodiversity with extinction.

AGL: African Great Lakes

INTRODUCTION

Straddling the equator in East Africa is one of the most remarkable freshwater features of our planet, the African Great Lakes (AGL) (**Figure 1a**). These lakes range from relatively shallow, saline, and alkaline, to some of the deepest and largest freshwater bodies on earth (**Table 1**). The three largest lakes (Tanganyika, Malawi, and Victoria) contain more than a quarter of the earth's, and >90% of Africa's, surface freshwater. The AGL also hold extraordinary ecosystems that collectively house some of the most diverse and renowned radiations of freshwater biota. The limnological properties of each of the AGL are strongly controlled by the interaction between tectonic (mostly rifting) and climatological processes and by the bedrock geology in each basin (Tiercelin & Lezzar 2002). Rifting is a long-term geological process that continually causes the earth's crust on the floor of the rift to subside, potentially allowing these lakes to persist for very long periods (>10⁷ years in extreme cases), much longer, for example, than the numerous glacial lakes at higher latitudes (Cohen 2003). Faulting associated with the rifting process has produced extremely

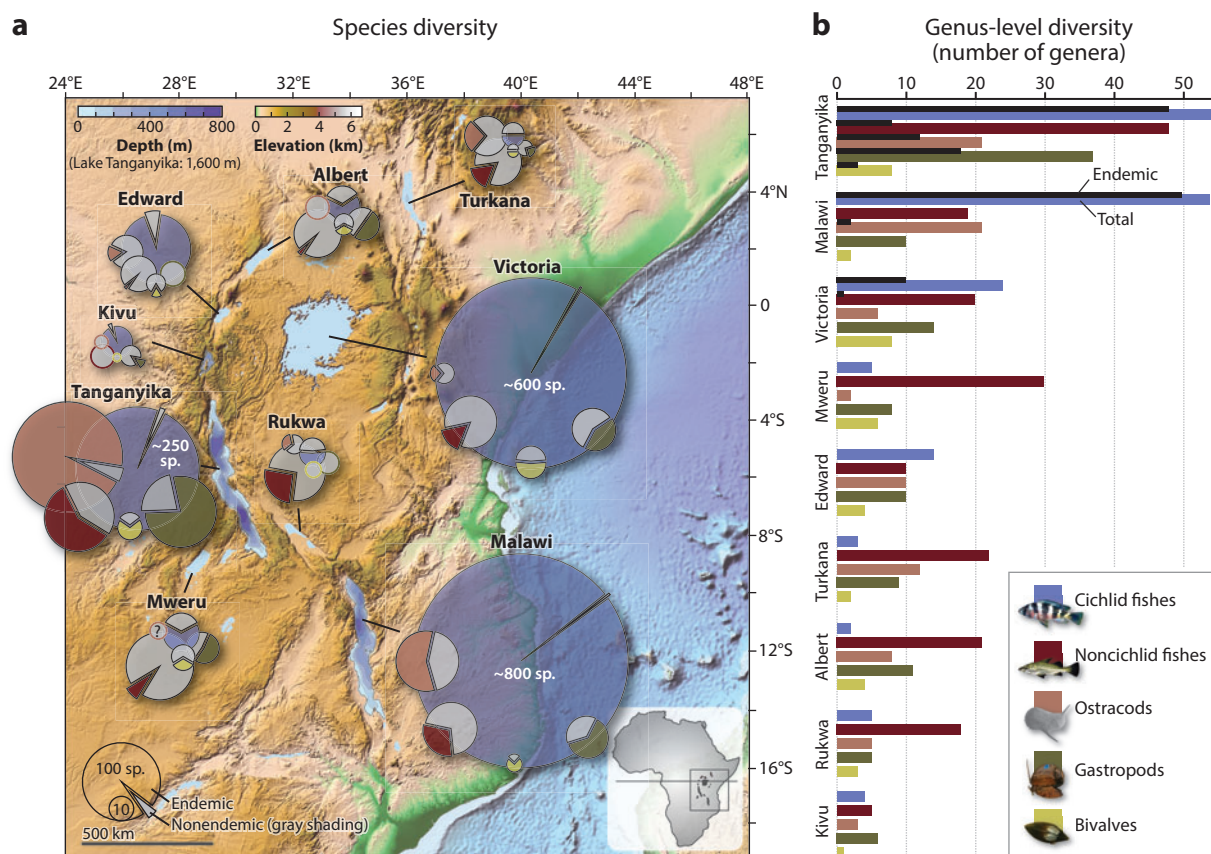


Figure 1

The African Great Lakes (AGL) and their faunas. (a) Map of the East African Rift showing the position of the nine extant AGL. For each lake, we indicate the number of species (and the fraction of endemics) within cichlid fishes, noncichlid fishes, ostracods, gastropods, and bivalves. For groups lacking endemics in a particular lake, the taxon is indicated by the colored border around the circle. (b) Bar graph showing the total number of genera for the same five clades in each lake, as well as the proportion that is endemic (black bars). Sources for species and genera numbers are given in **Supplemental Document 1** (follow the **Supplemental Material** link from the Annual Reviews home page at <http://www.annualreviews.org>).

Table 1 Environmental data summary of the nine extant African Great Lakes^a

Lake	Area (km ²)	Max. depth (m)	Depth of permanent stratification (m)	Transparency ^b	Conductivity (μS cm ⁻¹)	pH	Regional climate ^c	Basin age	Most recent drought and ecological crisis
Victoria	68,800	92	40–50 ^d	1–5 ^d	100	7.0–9.0 ^e	Subhumid to humid (800–2,000) ^e	~400 ka	~15–18 ka
Tanganyika	32,600	1,470	120–250	10–30	600–700	8.5–9.1	Subhumid (1,200) ^e	~9–12 Ma	3 Ma
Malawi	28,800	700	200–250	10–30	230–300	7.2 (bottom)–8.7 (surface)	Semiarid to humid (500–1,800) ^e	~5 Ma	~100 ka
Turkana	8,860	106	Completely mixed	1–13	3,000–5,000	8.8–9.4	Arid (150–300)	4–5 Ma	~15–18 ka
Albert	6,800	58	Completely mixed	2–6	700–750	8.9–9.5	Semiarid to subhumid (750–800)	~8 Ma	~15–18 ka
Mweru	4,350	37	? Completely mixed	~1	70–125	6.6–9.3	? Subhumid (~1,200–1,300) ^f	<2 Ma ^g	?
Rukwa	3,700	14	Completely mixed	<1	750–5,100 ^e	8.0–9.1	Semiarid (840)	5–10 Ma ^g	Twentieth century
Kivu	2,370	485	50–80	3.5–6.0	5,500 (bottom); 1,200–1,400 (surface)	6.8 (bottom)–9.0 (surface)	Subhumid (1,200–1,500)	~4.0–7.5 Ma	Holocene ^g
Edward	2,325	117	80–117 ^h	1.4–3.0	900	8.7–9.3	Subhumid (900)	~8 Ma	~15–18 ka

^aThe two Paleolakes, Obweruka (~7.5–3.0 Ma) and Manonga (~5.0–4.0 Ma), are not included, but Obweruka resembled Lake Tanganyika in size and depth and also drained into the Congo River, whereas Manonga was a smaller, shallower version of Lake Victoria located in Tanzania that drained toward the Indian Ocean. Question marks for Lakes Mweru and Rukwa indicate uncertainty because accurate data are lacking.

^bSecchi disk depth in meters.

^cWith average annual rainfall (mm/year) in parentheses.

^dThe depth of stratification in Lake Victoria declined during most of the twentieth century but seems to have increased slightly since the 1990s.

^eHighly variable in space and time.

^fData from nearest Climate Explorer station.

^gCaused by repeated injections of anoxic bottom water into surface waters.

^hRarely mixes to full depth.

steep and typically rocky escarpments, which in the larger and deeper lakes such as Tanganyika and Malawi often extend to hundreds of meters below the lake's surface (Tiercelin & Lezzar 2002). The extreme depths of some of the AGL, coupled with their year-round warm temperatures, cause a number of the lakes to be periodically or permanently stratified, with an upper, oxygenated mixolimnion and a more voluminous lower monimolimnion, which is anoxic but nutrient rich (Spigel & Coulter 1996). This stratification and the resultant oligotrophic conditions in surface waters (particularly in Lakes Tanganyika and Malawi today, and in Lake Victoria in the recent past) limit algal biomass and result in extraordinary water clarity, even in nearshore environments. This combination of age, geological history, lacustrine persistence, and limnological characteristics represents the backdrop for understanding the ecosystem characteristics and organismal diversity of the AGL.

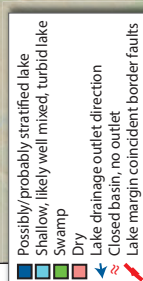
Most of the AGL lie directly within the African Rift Valley, a system of fault-bounded basins that extends from Djibouti in the north (12°N) to Malawi in the south (15°S). The rift originated from ongoing extension and gradual separation of the African and Somali continental plates, which started in the early Cenozoic (Tiercelin & Lezzar 2002). The African Rift Valley comprises two distinct and subparallel systems, the eastern and the western rift branches, whose positions have been determined by the upwelling of large-scale mantle plumes and their interaction with already existing zones of weakness in the earth's lithosphere. The eastern branch, extending from Djibouti to northern Tanzania, lies in a relatively arid region with abundant volcanic activity that disrupted and subdivided preexisting basins. As a consequence of the strongly negative precipitation-evaporation balance and of volcanic activity, most lakes in the eastern branch are comparatively small and shallow; many are saline and lack surface water outlets. Today, only one lake in the eastern rift (Turkana) (**Figure 1a**) qualifies as an AGL, defined here as lakes with surface areas greater than 2,000 km² (**Table 1**).

The western rift branch, which extends from northern Uganda to southern Malawi, is characterized by a much lower frequency of volcanic activity, extensive downfaulting, and much wetter climate regimes. These factors have allowed for the formation of larger, deeper, and more persistent lakes. All but one (Rukwa) can be characterized as freshwater lakes and possess surface outlets. Unlike the other AGL, Lake Victoria is not a rift lake but lies in a shallow depression between the uplifted shoulders of the two rift branches (**Figure 1a**). These uplifts have diverted former drainage systems into this broad, saucer-like basin, of which the center is occupied by Lake Victoria (Johnson et al. 1996). During the Late Miocene/Early Pliocene a similar but smaller lake, Paleolake Manonga, occupied the center of Tanzania (Harrison 1997) (**Figure 2**).

Interest in AGL faunas and their evolutionary history can be traced back to the earliest episodes of European exploration in tropical Africa, when scientists recognized the unusual nature of some of Lake Tanganyika's molluscs (Woodward 1859) and cichlid fishes (Boulenger 1898). Speculations about the origins of these animals spurred numerous expeditions in the late nineteenth and early twentieth centuries, which revealed the diversity and morphological disparity of fish, molluscs, and crustaceans inhabiting the AGL. In the mid-twentieth century, exploration resulted in a

Figure 2

Paleogeographic maps (*a–f*) of the AGL region showing hydrographic configurations of major lakes and rivers for six periods during the past 4 Ma. Numbers in white depict estimated water depths. Dashed blue lines indicate probably intermittent rivers; solid blue lines indicate major perennial rivers. The sources for preparation of these maps are given in **Supplemental Document 1**. Geographic basemaps were constructed from GeoMapApp (<http://www.geomapapp.org>). Abbreviations: AGL, African Great Lakes; ka, thousand years; L., Lake; LGM, last glacial maximum; Ma, million years; masl, meters above sea level; N, north; P-E, precipitation-evaporation; R., River; S, south.



Ecological

opportunity: a wealth of evolutionarily accessible biological resources (e.g., habitat, food) that are not (or poorly) used by other taxa

Sexual selection: the selection on mating behavior, either via competition for access to mating among members of one sex or via mate choice

Hybridization: the process of interbreeding between members of two distinct species

first series of monographic treatments on the faunas of Lakes Malawi, Victoria, and Tanganyika, which provided the initial taxonomic framework to raise questions about the origin of their extraordinary organismal diversity (e.g., Fryer & Iles 1972, Poll 1946). These papers also set the stage for an explosion of studies, spurred on by rapid advances in molecular techniques since the late twentieth century, that documented the evolutionary history of specific clades in the AGL, particularly among the cichlid fishes (e.g., Kocher et al. 1993, Meyer et al. 1990). Concurrent with the recent advances in phylogenetics and genomics, our understanding of the geological and paleoecological history of the AGL has augmented rapidly. Fossil collections from the precursors of the modern AGL have formed the grist for debates about tempo and mode of evolution (Van Bocxlaer et al. 2008, Williamson 1981). Additionally, long sediment cores and geophysical data have placed real constraints on the history and ecological continuity of the AGL, in the process allowing phylogenetic hypotheses to be tested and refined (Cohen et al. 2007, Johnson et al. 1996).

Our goal here is to highlight the extraordinary biodiversity and endemism that have arisen in these fascinating and often long-lived lakes. We emphasize the role AGL faunas (most notably, but not exclusively, the cichlids) have played in addressing key questions concerning evolutionary biology. Clades of AGL biotas have served as models for understanding the patterns and processes of diversification through integrative studies on extant and fossil faunas. We highlight the modes and mechanisms of speciation; the role of ecological opportunity, sexual selection, and hybridization; and the origins of morphological disparity; among others. We also review ecosystem functioning and provide a comparative synthesis on selected aspects of the natural history of AGL biotas. Finally, we summarize macroevolutionary patterns and demonstrate that the AGL are affected by many anthropogenic stressors at both global and regional scales, and that some of these stressors may compromise ecosystem stability and drive part of the extraordinary biodiversity to extinction.

AFRICAN GREAT LAKES: HOT SPOTS OF BIODIVERSITY

Patterns of Organismal Diversity

By any measure the AGL, particularly Lakes Malawi, Victoria, and Tanganyika, are extraordinary reservoirs of freshwater biodiversity (**Figure 1a**). A comparison of the combined diversity of fishes in the five most-species-rich AGL (~1,800 species, ~95% endemic) with that of the five North American Great Lakes (176 species, 3% endemic) (Hubbs & Lagler 2004) highlights this species richness, especially because the combined surface area of the AGL (~146,000 km²) is substantially smaller than that of their North American equivalent (~244,000 km²). Furthermore, the total number of species described from the AGL is likely underestimated because most of the lakes are only partially explored, and some taxa, particularly invertebrates, require more systematic study (Snoeks 2001, West et al. 2003).

Beyond the sheer taxonomic richness, remarkable endemism is observed within AGL basins. Much of the intralacustrine endemism relates to species with highly restricted geographic distributions, with some populations occupying only a few kilometers of shoreline (Baric et al. 2003, Snoeks 2001, West et al. 2003). Very few species occur in more than one of the AGL; for example, not a single cichlid species is naturally shared between Lakes Malawi, Victoria, and Tanganyika (Fryer & Iles 1972, Salzburger & Meyer 2004). A comparison of genus-level diversity and endemism provides a first-order perspective on the taxonomic diversity of the AGL (**Figure 1b**). These data highlight the distinctiveness of Lake Tanganyika, which houses more genera among many groups of organisms, with greater degrees of endemism and morphological disparity, in comparison to other AGL. Numerically, genus-level diversity and endemism of cichlids in Lake Tanganyika are roughly equaled by those of Lake Malawi, but the Tanganyikan cichlid assemblage consists of 12–16 tribes

and is genetically, morphologically, ecologically, and behaviorally more diverse than the faunas in Lakes Victoria and Malawi. These latter assemblages contain almost exclusively members of one of these tribes, the Haplochromini, plus a few species each of the more ancestral and only moderately radiating Tilapiini (Salzburger 2009, Salzburger et al. 2005). It remains controversial to what extent the extraordinary levels of phylogenetic diversity in the old Lake Tanganyika reflect a continuous amassing of taxa that evolved within the lake or an accumulation of relicts of older (perhaps pre-rift) diversification events, to which the lake served—because of its age and stability—as a refuge.

In general, the East African Rift presents an unparalleled system of quasi-replicate environments that allows the study of tempo and the mode of organismal diversification. Patterns and processes can be compared between distantly related taxa that occupy the same basin, between closely related taxa across basins, and holistically, integrating both in comparative approaches. We highlight these comparative approaches below; first we discuss the eco-insular nature of the fauna.

The Eco-Insular Nature of the AGL

The assemblages of cichlids and other taxa in the AGL are commonly referred to as species flocks—a term initially coined by botanists to connote island-type biotas of closely related species that flock together, i.e., that coexist in the same area (Greenwood 1984). Species flocks are characterized by their species richness, the shared origin of their members, their high levels of endemism, and their restricted geographic occurrence. The AGL are to aquatic organisms what oceanic islands are to terrestrial biotas: quasi eco-insular systems. Much like many oceanic islands, the AGL occur in clusters near tectonic hot spots, but many other features break the analogy between both systems. Because of the nature of the geological processes that form them, oceanic island chains include individual islands, which increase in age and maturity away from a hot spot. In contrast, the AGL do not show any systematic age or limnological progression with geography. Differences in basin formation, topography, and historical contingency give each basin its own dynamics regarding climate, age, ecosystem characteristics, and inhabiting biota. Another crucial difference is that lakes accumulate sediments, whereas oceanic islands are continuously exposed to erosion, i.e., a process obliterating geobiological evidence. This is particularly true for rift lakes, which are depositional centers with sinking floors that have accumulated rich archives of climate and ecosystem dynamics in sedimentary sequences that are often several kilometers thick (Cohen 2012). There is also an important difference with respect to colonization histories. Oceanic islands have typically been colonized after their formation by occasionally arriving long-distance dispersers, and within island chains from the older to the younger islands. The AGL, however, were independently colonized by freshwater biota inhabiting nearby areas, mostly from rivers to which the lakes were connected over time. Colonization may have happened at various times in a lake basin's history, for example, during the early phases of lake formation, after desiccation events, during drainage reversals, and during successful zoochoristic transport (see, e.g., Van Bocxlaer et al. 2008).

How Did the Spectacular Biodiversity Evolve?

The taxonomic diversity, endemism, and morphological disparity in many AGL biotas raise the question of how organismal evolution occurred in these unique environments. Much of this diversity is the product of evolutionary and, particularly in cichlids, adaptive radiation (see below). Hence, we first focus on adaptive radiation and its two main components, speciation and adaptation of the newly formed species to distinct ecological niches (Gavrillets & Losos 2009). Subsequently, we discuss morphological disparity, mechanisms of morphological evolution in the AGL, and recurrent patterns.

Eco-insular ecosystem: an island ecosystem that has limited ecological interactions with surrounding ecosystems and is isolated because of its drastically different habitats

Adaptive radiation: the rapid origin of new species from a common ancestor as a consequence of adaptation to distinct ecological niches

Natural selection:

the process by which the individuals with traits that confer survival or reproductive advantages increase in frequency over generations

Mutation-order speciation:

the evolution of reproductive isolation by the stochastic fixation of advantageous mutations in isolated populations that experience similar selection regimes

Ecological speciation:

the evolution of reproductive isolation as a result of divergent natural selection between populations adapting to different environments

Adaptive radiation. Much like oceanic islands, the AGL represent phenomenal laboratories of organismal evolution, with lineages diversifying rapidly into clades that display a multitude of new species. Such evolutionary radiations are considered adaptive if new reproductively isolated forms evolve rapidly and feature new phenotypes required to exploit various ecological niches (Gavrilets & Losos 2009, Schluter 2000). Adaptive radiations typically occur after the arrival of a founding population in a new environment with empty niches (ecological opportunity); after the evolution of a novel trait (key innovation), allowing the exploitation of new niches; and/or after the extinction of faunas in a way that effectively liberates formerly occupied niches (Gavrilets & Losos 2009, Schluter 2000). Both explicitly and implicitly, the faunas of the AGL have long been associated with the process of adaptive radiation (Fryer & Iles 1972). The cichlid fishes stand out as an unrivaled example of adaptive radiation (Kocher 2004, Santos & Salzburger 2012), but spectacular diversification is observed in several other groups of aquatic organisms that inhabit the rift (e.g., ostracodes and gastropods; Park et al. 2002, West et al. 2003, Wouters & Martens 2001), although for many of these radiations the adaptive nature has not yet been demonstrated.

Speciation. The faunas of the AGL, and the cichlids in particular, have long served as model systems to investigate Darwin's mystery of mysteries: the origin of species. For over a century, scientists have been puzzled by the extensive numbers of endemic cichlid species in the AGL, by the complexity of their life histories and biotic interactions, and by the mechanisms that led to the origin of these species assemblages (see, e.g., Fryer & Iles 1972, Kosswig 1947, Moore 1898, Worthington 1954). Two principal questions are: How could so many species have arisen in a relatively short period, and how is the high species diversity maintained within each lake (Salzburger & Meyer 2004)? In other words, how do speciation and extinction balance out? Many of the early debates centered around the first question (Regan 1921) and, instigated by Woltereck's (1931) hypothesis of *schizotypische Artsplitterung* (explosive speciation), around whether complete geographic separation (allopatry) was required for speciation. Despite decades of controversy on geographic modes of speciation (e.g., Fryer & Iles 1972, Kosswig 1947), all parties agreed that natural selection constitutes a pivotal component of speciation.

Speciation by natural selection can be broadly categorized into mutation-order speciation and ecological speciation (Schluter 2009). Whereas speciation during adaptive radiation is not restricted per se to a particular mode or mechanism, ecological speciation is generally considered the dominant mechanism (Schluter 2000), and clear-cut examples of ecological speciation exist in AGL cichlids: First, Seehausen et al. (2008) demonstrated that varying light conditions in Lake Victoria led to divergent selection on visual pigment (opsin) genes in the genus *Pundamilia*, which in turn affected sexual selection via female mate preference. Second, cichlid body plans, especially the morphology of their trophic apparatus, are strongly correlated with their habitat and food type specialization, suggesting that divergent natural selection played an important role in diversification (reviewed in Salzburger 2009). Third, too few geographic barriers seem present in the AGL, and mutation-order divergence is too passive a process to explain cichlid speciation rates, which are among the fastest known (McCune & Lovejoy 1998), without ecological speciation. Preliminary experimental data suggest that ecological differentiation also occurred in freshwater gastropods of the AGL (Gurdebeke & Van Bocxlaer 2013), but more research is needed to evaluate the relative importance of adaptive and nonadaptive components in evolutionary radiations of AGL biotas.

Other mechanisms such as hybridization and sexual selection have contributed to organismal diversification in the AGL. For example, several cichlid species are the product of introgressive hybridization between sometimes distantly related parental lines (Koblmüller et al. 2007, Salzburger et al. 2002). It has even been suggested that hybridization may be a precondition for adaptive

radiation (and ecological speciation), as it enhances genetic diversity and produces new (transgressive) phenotypes, thereby facilitating the potential for adaptive diversification (Seehausen 2004). Molecular phylogenetic data indeed suggest that hybridization preceded the radiations of cichlids (Joyce et al. 2011, Loh et al. 2013) and gastropods in Lake Malawi (Schultheiß et al. 2009). The phylogenies of several cichlid tribes in Lake Tanganyika also show signs of ancient hybridization (Koblmüller et al. 2007, Sturmbauer et al. 2010). Sexual selection via both female preference for male nuptial coloration and male-male competition has long been viewed as a driver of (sympatric) speciation in cichlids of the AGL, where sexual dimorphism is prevalent and numerous color morphs exist in many species (Maan & Sefc 2013, Seehausen & Schluter 2004, Turner & Burrows 1995). To what extent sexual selection alone can lead to speciation is a matter of debate, because it usually interacts with natural selection (Salzburger 2009, Seehausen et al. 2008).

Ecological opportunity. The relative importance of ecological opportunity (e.g., relative habitat stability, number of ecological niches, habitat heterogeneity driven by tectonic and/or climate variability) versus intrinsic biological factors in organismal diversification in the AGL remains under discussion. The AGL are unusual in that they house species flocks in so many taxonomic groups, suggesting that ample ecological opportunities are provided by the AGL and that these opportunities play a pivotal role in the evolution of AGL biota. Addressing this question for cichlids, Wagner et al. (2012) found that the most consistent predictors of diversification include both extrinsic (surface area and depth of lake) and intrinsic (sexual dichromatism) factors. A comparison of riverine and lacustrine faunas suggests that lakes provide much larger ecological opportunities than rivers do; hence, perhaps the most drastic reduction of extrinsic opportunities in the AGL occurs with the entire desiccation of lakes (e.g., the Late Pleistocene desiccation of Lake Victoria and other lakes in the region; Beuning et al. 1997, Johnson et al. 1996) (**Figure 2**). However, other events, such as the occasional large-scale mixing of quasi-permanently stratified lakes, causing extensive asphyxia in the upper water column can also drive extinction events. Such extinctions can in turn create new ecological opportunities when aquatic environments restabilize. Lake Kivu has such unstable limnological conditions and, as a result, an impoverished fauna, despite it being the third deepest of the AGL (**Table 1, Figure 1**).

The notion that long-term persistence and ecological stability have allowed some lakes to amass biotas with high levels of genetic diversity and morphological disparity appears to be an important macroevolutionary pattern in the AGL (e.g., Genner et al. 2007; implicitly also in Wagner et al. 2012). Molecular diversity and morphological disparity in the three largest African lakes certainly reflect the time elapsed since each lake's last major ecological crisis (Cohen et al. 2007) (**Table 1, Figure 3**), and none of the smaller, more unstable lakes rivals the large lakes in organismal diversity and morphological disparity. We come back to this issue below but want to highlight here that intrinsic and extrinsic factors often interact with each other in speciation. For example, lake-level fluctuations change not only the area and diversity of available benthic habitats, but also other extrinsic properties, such as water clarity, that affect mate recognition and optically driven sexual selection in cichlids—an intrinsic factor that, as mentioned above, has promoted cichlid diversification.

Intrinsic factors. Beyond the intrinsic factors already discussed in relation to sexual selection, two other explanations for the evolutionary success in cichlids have been provided: something special in their genomes and evolutionary innovations (reviewed in Salzburger 2009). The sequencing of five genomes of East African cichlid fishes revealed that the explosively radiating cichlid clades in Lakes Victoria, Malawi, and Tanganyika show characteristic genomic differences compared with the Nile tilapia—a member of a more ancestral and less species-rich cichlid lineage—and

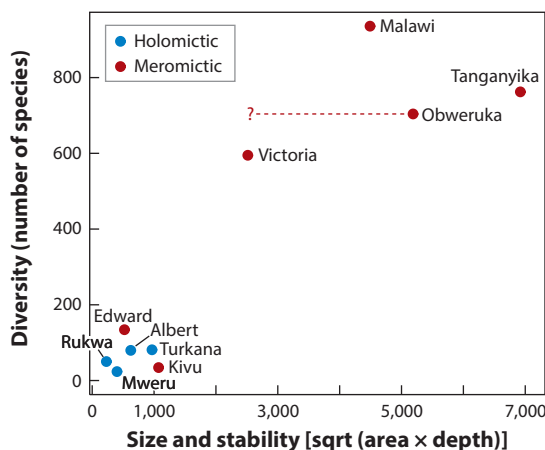


Figure 3

A positive correlation exists between lake size and ecosystem stability versus diversity (number of species) in the African Great Lakes. This rough metric clearly indicates why Lakes Malawi, Tanganyika, and Victoria have traditionally been considered ancient lakes (see Martens 1997); long-lived Paleolake Obweruka probably falls within this range, too. Compared with that of other ancient lakes, ecosystem stability for Lake Victoria has been limited. The comparably great diversity in this lake may be explained by its invasion history, intrinsic biological factors, and the saucer-like basin morphology. That morphology may have resulted in (on average) larger distances and less gene flow between populations. Definitions: holomictic, completely mixed; meromictic, permanently stratified.

other teleosts. These differences may be associated with a differential propensity to diversify: The radiating cichlid clades of the AGL show accelerated rates of molecular evolution, a greater number of duplicated genes, divergence in gene expression, and gene regulation that occurs through novel miRNAs (Brawand et al. 2014). The pharyngeal jaw apparatus of cichlids is considered a key innovation that facilitated the group's evolutionary success (Liem 1973). This structure acts as a second set of highly specialized jaws, which are functionally decoupled from the oral ones, thereby increasing trophic versatility.

Patterns and Processes of Morphological Evolution

As mentioned above, species flocks of AGL biota display—beyond great diversity—much morphological disparity, and here we explore mechanisms that have generated this phenotypic variation.

Niche diversification. The emergence of diverse phenotypes, often highly correlated with particular ecological niches, is a key feature of the AGL faunas. Quantitative analyses of phenotypic evolution in association with niche diversification have focused mainly on cichlids: Among the cichlids of Lake Tanganyika, overall body morphology correlates with macrohabitat (Clabaut et al. 2007, Muschick et al. 2012), whereas the morphology of the trophic apparatus, including the lower pharyngeal jaw, correlates with feeding mode (Muschick et al. 2012), suggesting that adaptation to available niches is a prominent driver of both morphological evolution and diversification. Gastropod species flocks from Lake Malawi (e.g., *Janistes* spp.) display differences in shell morphology and, to lesser extent, feeding morphology along a bathymetric gradient (Mandahl-Barth 1972).

Evolution in stages? The cichlids of Lake Malawi have served as a template for the stage model of adaptive radiation (Danley & Kocher 2001, Streelman & Danley 2003), which suggests that in

Pharyngeal jaws:

modification of the branchial skeleton in which an upper and lower bone structure function for feeding, complementing the oral jaws

the initial phases of a radiation, divergence occurs with respect to macrohabitats (e.g., sandy versus rocky habitats), then with respect to microhabitats, and finally with respect to mating traits (see also Gavrillets & Losos 2009). Although the phylogenetic structure of the cichlid species flocks of Lakes Malawi and Tanganyika, in which deeper splits separate major ecological clades, appears to support this trend (Danley & Kocher 2001, Kocher 2004), a quantitative analysis (Muschick et al. 2012) found no support for this model in Tanganyikan cichlids, suggesting that ecomorphological disparity in body shape and the pharyngeal jaw was always high throughout the radiation. A related question is whether morphological evolution follows an early-burst model (Gavrillets & Vose 2005), which must still be examined with data for AGL biotas.

Standing genetic variation. Evidence is accumulating that rapid morphological divergence may benefit from standing genetic variation rather than new mutations. Standing genetic variation may persist via the retention of ancestral polymorphism and through hybridization (Barrett & Schluter 2008), both of which are commonly observed in AGL biotas (see, e.g., Joyce et al. 2011, Loh et al. 2013, Schultheiß et al. 2009). A study of genome-wide markers in cichlids revealed unexpectedly high degrees of standing variation (Loh et al. 2013), which are possibly maintained by occasional gene flow between riverine and lacustrine taxa over time and across large geographic regions.

Epigenetics and phenotypic plasticity. Morphological plasticity in the body plan of AGL biota may relate to developmental switches, gene regulation, and epigenetics, as well as ecophenotypy. Adaptive phenotypic plasticity and marked switches in gene expression have been documented in cichlids, e.g., in the pharyngeal jaws in response to different food sources and the hardness of the diet (Gunter et al. 2013) and in their behavior with respect to social rank (Aubin-Horth et al. 2007, Burmeister 2007). Although the relative importance of phenotypic plasticity in evolution is still under debate, the phenomenon can generate adaptive phenotypic variation; hence, it is increasingly recognized as an agent of divergent selection, speciation, and even radiation. In freshwater molluscs of the AGL, mainly in pulmonate gastropods (Standley et al. 2011), such ecophenotypes have also been recognized.

Recurrent Patterns

Upon studying morphological disparity through space and time, two main recurrent patterns have been observed: iterative evolution and morphological convergence.

Iterative evolution. The AGL present a phenomenal setting of quasi-replicate lake systems in which closely related faunas evolved. Given that similar mechanisms have allowed the biodiversity in different lakes to evolve, iterative evolution is expected and observed at various scales (**Figure 4**). Overall, the mollusc faunas of the lakes that have successively occupied the Turkana Basin are highly similar (Van Bocxlaer et al. 2008), and these similarities led earlier workers (Williamson 1981) to assume ancestor-descendant relationships. In Paleolake Obweruka—which existed in the Albertine Basin ~7.5–2.5 Ma ago, was comparable in size and depth to Lake Tanganyika, and drained toward the Congo—iterative evolution of ornamentation is observed in several families of freshwater molluscs (Ampullariidae, Viviparidae, and Pachychilidae) (**Figure 4b**). Levels of diversity and morphological disparity in the molluscs that inhabited this ancient basin resembled those of modern Tanganyikan species (Van Damme & Pickford 2003, West & Cohen 1996), but **Figure 4b** illustrates that taxa appear to have had low persistence and quick turnovers (hence increasing chances for iterative evolution). The adaptive radiations of cichlids in several lake basins are another example: In Lakes Tanganyika and Malawi, a whole set of similar cichlid ecotypes

Epigenetics:

heritable changes in gene activity (e.g., gene expression) that are not caused by changes in the DNA sequence

Ecophenotypy:

nonheritable modification of the phenotype of an organism resulting from environmental influences

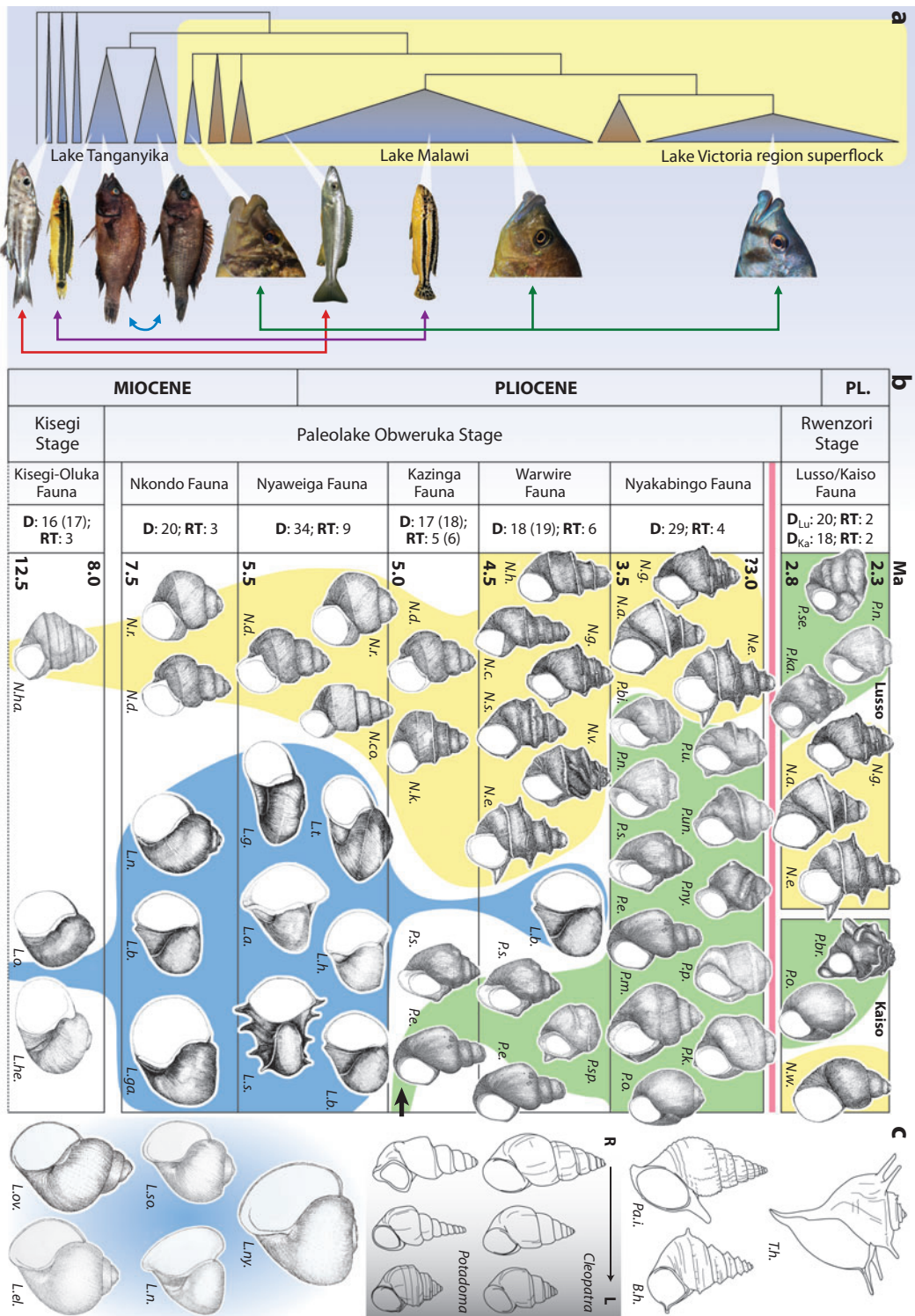
have evolved independently and in parallel (Kocher et al. 1993), even though those of Lake Tanganyika belong to several (and sometimes ancient) tribes and those in Malawi exclusively to the Haplochromini, which evolved later. Cichlid species with hypertrophied lips have evolved multiple times in Lakes Victoria, Malawi, and Tanganyika (**Figure 4a**), and even in non-African cichlid radiations (Colombo et al. 2013, Salzburger 2009). The prevalence of iterative evolution in the AGL suggests that evolution is to some extent deterministic.

Morphological convergence. Morphological convergence is a widespread phenomenon in quasi-replicate adaptive radiations (e.g., Mahler et al. 2013) and frequently observed in the AGL (Kocher et al. 1993, Muschick et al. 2012). Early studies focused on the ornamented molluscs of Lake Tanganyika, which in some cases bear striking resemblances to marine molluscs (e.g., Moore 1898), but convergence on marine body forms is also evident in some Tanganyikan copepods, ostracodes, bryozoans, and crabs (Brooks 1950, von Sternberg & Cumberlidge 1999, Wouters & Martens 2000). The most illustrative examples of convergent evolution between lakes are the cichlids and molluscs of Lakes Victoria, Malawi, and Tanganyika (e.g., Brooks 1950, Kocher et al. 1993, Poll 1946, Regan 1921, Van Damme & Pickford 2003) and the Afrotropical freshwater crabs (Daniels et al. 2006). Within the fauna of a single lake, evolutionary convergence in overall morphology has been found (**Figure 4c**) (Mandahl-Barth 1972, Muschick et al. 2012, Rüber & Adams 2001) and related to specific traits such as biparental mouthbrooding (Koblmüller et al.

Figure 4

Diversity and disparity in cichlids and molluscs of the African Great Lakes. (a) Consensus phylogeny based on mitochondrial DNA of the main East African cichlid lineages. The images depict convergent species between (green, purple, and red arrows) and within (blue arrow) lakes. Group size in the phylogeny represents the number of species of the respective clade, the yellow box marks the tribe Haplochromini, and brown clades contain riverine representatives. (b) Stratophenetic representation of the three largest caenogastropod radiations (*Neothauma*, in yellow; *Lanistes*, in blue; and *Potadoma*, in green) in Paleolake Obweruka through time (epochs and stages). Radiations in these genera take place at different times, but in each radiation some strongly ornamented taxa evolved from weakly ornamented ancestors. For each fauna, mollusc diversity (D) and the number of species that range through the respective time interval (RT; i.e., it is present in the earlier and subsequent intervals) are indicated. The ratio between D and RT indicates a quick succession of species (many originate and wither during the same faunal interval). The pink line indicates faunal extinction linked to the uplift of the Rwenzori Mountains; the arrow indicates the point at which *Potadoma* invaded the basin. (c) From top to bottom: a selection of strongly ornamented caenogastropods from Lake Tanganyika; morphological convergence as riverine *Cleopatra* and *Potadoma* species (R) evolve into lake-adapted species (L) in different paleolakes of the Turkana Basin; and the modern *Lanistes* species flock from Lake Malawi. Radiations of *Lanistes* in Paleolake Obweruka and Lake Malawi show striking convergence but also marked differences (no ornamented taxa in Lake Malawi). Specimens are not depicted to scale. Data and images are from (a) Salzburger 2009; (b) Van Damme & Pickford 1995, 1999, 2003, with kind permission of Springer Science+Business Media; (c) Van Bocxlaer et al. 2008, 2012b.

Ranging through indicates the number of species present in Kisegi, Oluka, and Nkondo times for the Kisegi-Oluka fauna; for the Lusso and Kaiso fauna it reflects species present in the Lusso-Kaiso and Nyakabingo periods as well as the subsequent unstable Nilotic period (not shown). Depicted taxa: (a) from top to bottom: *Haplochromis chilotes*, *Melanochromis labrosus*, *Melanochromis auratus*, *Rhamphochromis* sp. (photo credit: E. Schraml), *Lobochilotes labiatus*, 'Ctenochromis' *bentibicola*, *Neolamprologus prochilus*, *Julidochromis ornatus*, *Bathybates graueri* (images: Salzburger Lab). (b) Abbreviations: *Lanistes asellus* (L.a.), *L. bishopi* (L.b.), *L. gautieri* (L.ga.), *L. gigas* (L.g.), *L. badatoi* (L.b.), *L. beynderycxi* (L.be.), *L. nkondoensis* (L.n.), *L. olukaensis* (L.o.), *L. senuti* (L.s.), *L. trochiformis* (L.t.), *N. adami* (N.a.), *N. carinatum* (N.c.), *N. concavum* (N.co.), *N. dubium* (N.d.), *N. edwardianum* (N.e.), *N. ganabli* (N.g.), *N. battlingbi* (N.ba.), *N. beinzelini* (N.b.), *N. kazingae* (N.k.), *N. rotundum* (N.r.), *N. semilikiense* (N.s.), *N. vermeiji* (N.v.), *N. waylandi* (N.w.), *P. bifidicincta* (P.bi.), *P. brevissima* (P.br.), *P. emerenciae* (P.e.), *P. kanyatsiae* (P.ka.), *P. kyeoroensis* (P.k.), *P. mupandae* (P.m.), *P. nageli* (P.n.), *P. nyakabingoensis* (P.ny.), *P. olivoidea* (P.o.), *P. plicata* (P.p.), *P. sebugoroensis* (P.s.), *P. sengae* (P.se.), *P. spinifera* (P.sp.), *P. undulosa* (P.u.), *P. uncinata* (P.un.) (images: D. Van Damme). (c) Abbreviations: *Tiphobia borei* (T.b.), *Paramelania iridescens* (Pa.i.), and *Bathania bowesi* (B.b.). *Lanistes* cf. *ovum* (L.ov.), *L. cf. ellipticus* (L.el.), and *L. solidus* (L.so.) from Lake Malawi resemble *L. nkondoensis* and *L. olukaensis* from Paleolake Obweruka; *L. nasutus* (L.n.) resembles *L. asellus* and *L. badatoi*; and *L. nyassanus* (L.ny.) resembles *L. gautieri* and *L. bishopi* (images: B.V.B.). Abbreviation: PL., Pleistocene.



2004), the jaw apparatus (Muschick et al. 2012), and color patterns (Duftner et al. 2007) in cichlids, and ovoviviparous/viviparous reproduction in molluscs (Michel 1994).

Meromictic:

describes lakes that are quasi-permanently stratified and hence have an upper oxic (usually nutrient-poor) mixolimnion and a lower anoxic, nutrient-rich monimolimnion

Holomictic:

describes lakes that mix completely at least on a yearly basis, so that temperature and density become uniform from top to bottom

Coevolution:

evolution of unrelated species in parallel because each party exerts selective pressures on the other, thereby linking each other's evolution

COMMUNITY STRUCTURE AND ECOSYSTEM FUNCTIONING

In the meromictic AGL, multicellular life is restricted to the upper, oxygenated water column (mixolimnion) and depends heavily on mixing regimes, including the balance of nutrient fluxes between the pelagic and benthic ecosystems and between onshore and offshore productivity (too little mixing leads to starvation, too much to asphyxia; see, e.g., O'Reilly et al. 2003, Vadeboncoeur et al. 2011, Van Bocxlaer et al. 2012b). The shallower or more exposed AGL are holomictic. They lack the buffering capacity of the deeper, anoxic waters (monimolimnion) and are therefore more susceptible to climatic fluctuations and geological events. However, all AGL are susceptible to oxygen depletion (locally or at larger scales) because at tropical temperatures a trade-off exists between decreasing oxygen solubility and increasing respiration rates, and because seasonal nutrient abundance (recycling from the monimolimnion or via runoff) can result in oxygen-consuming algal blooms. Hence, ecosystem functioning within the AGL depends on a fragile balance between many complex feedback systems within the lake, in the basin, and beyond.

Fryer (1959) presented an exemplary study of ecosystem functioning in Lake Malawi and highlighted differences between community structure on rocky versus sandy shores. This study and others (Michel et al. 2004, Salzburger & Meyer 2004, Seehausen 2006, Vadeboncoeur et al. 2011) suggest that several macroecological principles apply to the AGL: (a) Taxonomic diversity tends to increase with area (species-area effect), (b) more ecological niches (i.e., presence of ecological opportunity) allow greater taxonomic diversity, and (c) the degree of ecosystem stability determines the periods during which adaptation can occur. Generally, greater lake size correlates with greater niche diversity (though dependent on niche heterogeneity), and greater volume and depth increase buffering capacities, so that larger and deeper lakes have a greater stability and more biodiversity (**Figures 1** and **3**). Below, we highlight some remarkable ecological interactions in the AGL.

Coevolution is a central process driving natural selection and shaping the structure and function of communities (Brockhurst & Koskella 2013). As an agent structuring biological diversity, the prevalence of coevolutionary dynamics (e.g., between predator and prey or between parasite and host) potentially explains the difference in ecological interactions in the AGL and other surrounding waterbodies. Most of the evidence for coevolutionary interactions in freshwater is obtained from large and long-lived rivers and lakes (Vermeij & Covich 1978). Lake Tanganyika in particular represents a renowned system for the study of predator-prey interactions (e.g., Nori 1997, West & Cohen 1996). The iterative evolution of ornamented gastropods in Paleolake Obweruka (**Figure 2**) has also been attributed to predator-prey coevolution, but with characids and various catfish as predators instead of the molluscivorous crabs and cichlids of Lake Tanganyika (Van Damme & Pickford 2003). Intriguing indications for this coevolutionary escalatory arms race over time periods of about 10^5 years exist for intervals in the past ~ 4.5 Ma, when this paleolake was deep and permanently stratified. However, although the mollusc and fish (Stewart 2001) faunas diversified rapidly, the interaction mechanisms and timing of morphological change and coevolution are not completely understood (Van Damme & Pickford 1999, 2003).

A relatively poorly explored issue in AGL research is the ability of taxa to act as ecosystem engineers (see Harmon et al. 2009). One example is that Tanganyikan cichlids use and, in many cases, accumulate mollusc shells as breeding substrate and shelter (Sato & Gashagaza 1997). Intact and unoccupied shells are a limited resource, and fish dig up shells and keep them on the surface, often for $>1,000$ years, which is a behavior that strongly affects the composition of benthic substrates. Partly because of these interactions, Lake Tanganyika has much more

mollusc-rich sediments in its littoral zone compared with other AGL, and some snails, crabs, and abundant and diverse sponges live, often exclusively, on these shell beds (McGlue et al. 2010).

COMPARATIVE AND INTEGRATIVE BIOLOGY

Biogeography

As mentioned above, the tectonic and climatic history of East Africa has played a major role in shaping the patterns of diversity observed in the AGL today. Our knowledge of this history is rapidly evolving, especially through the recent and ongoing efforts to recover long drill cores from both extant lakes and paleolake deposits (Cohen 2012). We synthesize our current understanding through a series of snapshot reconstructions of the lakes (and, to the limited extent that they are known, river drainages) over the past 4 Ma (**Figure 2a-f**), which demonstrate the transience of freshwater connections and draining patterns through time as the rift developed. Overall, lakes could be categorized as more ecologically stable (e.g., Lake Tanganyika) or as systems with limited ecological stability (e.g., Lakes Victoria and Kivu; Schultheiß et al. 2009). The fauna of lakes in the first category usually is dominated by species flocks endemic to the lake basin, which may display marked spatial structuring, and potential relict organisms. Lakes in the second category normally contain proportionally more taxa inherited from larger-scale biogeographical connections (i.e., species scatters or nonmonophyletic groups of unrelated lineages), because more limited intralacustrine speciation occurred.

Patterns within lake basins. Variation in limnological stability due to a history of lake-level fluctuations has been a principal driver of organismal evolution in the AGL. Depending on basin topography, dramatic lake-level drops during arid phases in East Africa may have resulted in the isolation of habitat stretches or even the separation of one lake into smaller lakes confined to sub-basins (see, e.g., Danley et al. 2012). Compelling evidence for such a scenario comes from Lake Tanganyika, as studies on the rock-dwelling, nearshore cichlid genus *Tropheus* demonstrate that subclades are confined geographically in a way that reflects the three sub-basin bathymetric structure of the modern lake (Baric et al. 2003, Sturmbauer et al. 2001). The simultaneous explosive radiation in subclades is most parsimoniously explained as resulting from the isolation of numerous founder populations.

The evolutionary consequences of rapidly rising lake levels represent a somewhat different within-lake response to changing climatic conditions. For example, populations occupying different regions within a basin may become further separated from one another as the lake expands, which could result in diversification via isolation by distance and the evolution of ring species. Populations at opposite sides of a lake may also get isolated when intrabasin ridges that previously served as dispersal corridors become submerged within the anoxic deep waters of the lake. Following the dramatic rise of Lake Malawi ~100 ka ago (**Figure 2c**), the progressive isolation of numerous rocky islands allowed divergence in populations of the *Pseudotropheus* (*Maylandia*) species complex (Genner et al. 2010). Populations within this complex have different male nuptial colors, and most of them mate assortatively. The geographic restriction of haplotypes to individual or closely linked islands indicates that dispersal was limited (some geographic isolation) and that cladogenesis may have occurred in parallel in the organisms of different island clusters. Viviparid gastropods from Lake Malawi likewise show a demographic and spatial expansion associated with rising lake levels and, as a result, increased availability of sandy littoral substrates (Schultheiß et al. 2011).

Even relatively stable AGL, such as Tanganyika and Malawi, have faunal exchanges with the surrounding areas, e.g., because of changes in hydrographic connectivity between adjacent basins

Isolation by distance:
genetic differentiation
increases with
geographic distance

Ring species:
reproductively isolated
populations connected
by a geographic ring of
populations that can
interbreed

Highstand: a time interval when a lake's surface elevation is raised as a result of climatic or other mechanisms

as rifting proceeds (**Figure 2**). For example, several Tanganyikan cichlid clades contain derived taxa that occur exclusively in the Malagarasi River or the Congo River (Salzburger et al. 2005, Sturmbauer et al. 2010). Hence, more faunal exchange may occur between the AGL and their surroundings than is usually recognized. Nevertheless, because of the large buffering capacity of these stable AGL, compared with their surrounding waterbodies, it is also conceivable that taxa may persist in these lakes long after they have been eliminated elsewhere. Selective survival in the AGL can hence result in the occurrence of endemic relict taxa that may have had drastically different distributions and/or diversity in the past. The viviparid gastropod genus *Neothauma* is currently monotypic and confined to Lake Tanganyika, but as **Figure 2b** documents, it comprised numerous species in Paleolake Obweruka.

Larger-scale biogeographical patterns. In some AGL, wholesale ecosystem reorganizations have occurred after earlier ecosystem calamities. The newly invading fauna usually arrives from interbasinal dispersal, which depends strongly on the climatic and tectonic history of the basin: Beyond topographical changes (**Figure 2**), cycles of moisture and aridity in East Africa (see Donges et al. 2011, Trauth et al. 2005) have periodically increased chances for the dispersal of terrestrial and aquatic organisms (Danley et al. 2012, Van Bocxlaer et al. 2008, Williamson 1985). Perhaps the most conspicuous pattern caused by rifting and associated drainage reversals is that relatively deep phylogenetic splits between clades are often confined to either the eastern or the western side of the western branch of the East African Rift (Salzburger et al. 2005, Schwarzer et al. 2012), for which a spatially and temporally explicit biogeographic model has recently been proposed (Schultheiß et al. 2014).

A clear example of altered dispersal possibilities due to changes in the climate-moisture balance is the intermittent connectivity between upstream and downstream lakes. Evidence for highstands and spillover events during humid periods, as well as for associated interbasinal dispersal, exists in the fossil and modern ostracode and mollusc faunas of the Rukwa and Tanganyika Basins. Paleolake Rukwa was at a highstand on multiple occasions during the Quaternary, and it intermittently spilled over into Lake Tanganyika. This hydrographic connection allowed faunal exchange of taxa that were previously endemic to a single lake (Cohen et al. 2013).

The combination of climatic and tectonic events in the redistribution of aquatic biota over Africa is perhaps best recorded in the fossil record of the Turkana Basin, where a succession of paleolakes existed (Feibel 1997). Aquatic invasions in this basin coincide with wet periods, and topographic changes have allowed invasions of taxa with faunal affinities that have alternated over time between Congolese and Nilotic (Van Bocxlaer et al. 2008). Perhaps the most remarkable invader was a freshwater stingray, which colonized the basin from the Indian Ocean when a southerly outflow existed (i.e., Paleolake Lorenyang ~2.0 Ma; see **Figure 2e,f**) (Feibel 1993). In the early Holocene and perhaps other periods, the Turkana Basin had an outflow to the Nile River, introducing numerous fish and invertebrates from the north (Feibel 2011).

A noteworthy modern example for dispersal via hydrographic connections is provided by the colonization histories of the large clade of haplochromine cichlids, which constitute most of the extant fish diversity of Lakes Victoria, Edward, Albert, Kivu, and other nearby waterbodies, the so-called Lake Victoria region superflock (LVRS) (Verheyen et al. 2003). All these lakes, except for Kivu (and possibly Edward), were completely desiccated during the Late Pleistocene [last glacial maximum (LGM); e.g., Beuning et al. 1997, Johnson et al. 1996] (**Figure 2b**), when aridity was widespread in East Africa. Although the initial diversification and origin of some of the major lineages within the LVRS clearly predate the Late Pleistocene desiccations (Elmer et al. 2009, Verheyen et al. 2003), the extensive drought caused severe bottlenecks (Elmer et al. 2009). The deep Lake Kivu appears to have served as a refugium for the genetic diversity of the

LVRs during aridity (Verheyen et al. 2003), and major bursts of diversification in the superflock most likely postdate the rise of lake levels across the region after ~15 ka.

Comparative Patterns of Diversity

Up to now, most efforts to compare patterns of diversity in the AGL were driven by the search for how biodiversity originated. As we addressed that subject earlier, we only briefly highlight two current topics here.

Did most endemic taxa in the AGL evolve within extant lakes or prior to their formation?

The origin of biodiversity (intralacustrine versus independent invasions), especially for the molluscs of Lake Tanganyika, is a question that has been the subject of considerable debate (see above). Some authors suggest that most gastropod lineages in this lake diverged from one another through intralacustrine radiation (West & Michel 2000), but others argue that much diversity originated before the formation of the Tanganyika Basin, as many endemic taxa are part of groups that may have evolved elsewhere and arrived into the lake by migration or because riverine populations were captured by the emerging lake (Wilson et al. 2004). This issue remains contentious for Lake Tanganyika, but not for Lake Malawi, where gastropod diversification occurred primarily within the lake (Schultheiß et al. 2009, 2011).

Importance of extrinsic versus intrinsic factors. The relative importance of intrinsic and extrinsic factors in evolutionary radiations is another controversial issue that can be examined with comparative data. About 20 families of fish are present in Lakes Victoria, Malawi, and Tanganyika; some underwent intralacustrine radiation in at least one of the AGL, but others did not. In Lake Tanganyika, for example, small species flocks of spiny eels (Mastacembelidae), Nile perches (Latidae: *Lates* spp.), and squeaker catfish (Mochokidae: *Synodontis* spp.) exist (Coulter 1991). Yet none of these fish radiations rivals the diversity in Cichlidae, which radiated at least three times, largely independently (in Lakes Victoria, Malawi, and Tanganyika), and in a way that outnumbers any other species flock of fishes in the AGL by at least an order of magnitude. This comparison demonstrates the power and relevance of intrinsic biological factors.

Diversity and Disparity Through Time

Clades in the AGL have waxed and waned through time, and fluctuations are observed likewise in disparity. Although diversity and disparity are not necessarily correlated, the fossil record of the AGL suggests that the most taxonomically diverse assemblages were also the most morphologically diverse (e.g., Van Damme & Pickford 1999, 2003) and that cladogenesis in specific clades usually occurred after the waning of others (Figure 4b). This observation suggests that ecological opportunities are often created by ecosystem change and (local) extinctions (e.g., Van Bocxlaer et al. 2008). For example, the documentation of several extinct cichlid genera (Stewart 2001) testifies to earlier cichlid radiations in the AGL. When tectonic activity that initiated the uplift of the Rwenzori Mountains ~2.8 Ma disrupted Paleolake Obweruka, the ensuing ecological destabilization caused multiple extinctions. Some molluscs and probably fish initially survived in Paleolakes Kaiso and Lusso, the precursors of Lakes Albert and Edward, respectively, but eventually their diversity collapsed (Van Damme & Pickford 1999, 2003; Van Neer 1992) (Table 2).

Overshooting and extinction. When studying extant clades that underwent evolutionary radiation, evolutionary ecologists have observed overshooting, i.e., that young radiations often contain

Table 2 Examples of extinct genera in the freshwater fauna of the African Great Lakes^a

Genus	Family	Occurrence	
		First	Last
Fishes			
<i>Sindacharax</i>	Characidae	EM	700 ka
<i>Semlikiichthys</i>	Latidae	EM	EPL
<i>Dasyatis</i> ^b	Dasyatidae	~1.9 Ma	~1.2–0.8 Ma
<i>Bunocharax</i>	Characidae	MM	PL
<i>Nkondobagrus</i>	Bagridae	EP	EP
<i>Kalptochromis</i>	Cichlidae	EM	EM
<i>Nderechromis</i>	Cichlidae	EM	EM
<i>Palaeochromis</i>	Cichlidae	LM	LM
<i>Palaeofulu</i>	Cichlidae	EM	EM
Bivalves			
<i>Pseudodiplodon</i>	Unionidae	~2.6 Ma	~2.6 Ma
<i>Pseudobovaria</i>	Unionidae	LM	1.5–1.2 Ma
<i>Grafunio</i>	Unionidae	EPL	EPL
<i>Gautieraia</i>	Unionidae	LM	EP
<i>Nkondonaia</i>	Unionidae	LM	LM
<i>Obwerukunio</i>	Unionidae	EP	EP
Gastropods			
<i>Kaya</i>	Viviparidae	~7.5 Ma	~2.6 Ma
<i>Ellinoria</i>	Thiaridae	LM	EP
<i>Heynderyxia</i>	Thiaridae	TM	EP
<i>Mohariella</i>	Pomatiopsidae	MM	LM

^aReferences are provided in **Supplemental Document 1**.

^bIndicates local extinction.

Abbreviations: EM, Early Miocene; MM, Middle Miocene; LM, Late Miocene; TM, Terminal Miocene; M, Miocene; EP, Early Pliocene; LP, Late Pliocene; EPL, Early Pleistocene; PL, Pleistocene.

more species than old radiations do. Current explanations are that speciation rates may decrease over time as more niches become occupied and species become more specialized (the abovementioned early-burst scenario), and that extinction rates increase over time (Gavrillets & Losos 2009). Although the cichlids of Lakes Victoria, Malawi, and Tanganyika follow a trend of overshooting, there is little evidence that speciation rates in the old Lake Tanganyika decreased over time (Day et al. 2008). This finding may suggest a prominent role for (background) extinction either by stochastic events or by failure to keep pace with changing environments (evolutionary loss to the Red Queen).

MACROEVOLUTIONARY TIMESCALES

In addition to the exceptional extant biodiversity, the thick sedimentary sequences in most AGL contain excellent fossil archives of how organismal diversity and disparity have changed over time, and how communities and ecosystems developed as rifting and climate change proceeded. The study of these sediments and their fossil remains has drastically altered our perception of organismal evolution, historical biogeography, rates of evolution (e.g., by the time calibration

Red Queen hypothesis:

evolutionary hypothesis proposing that organisms must constantly adapt to gain reproductive advantage in the face of competition and other biological interactions

of molecular phylogenies), and ecosystem functioning over time. Hence, these archives form the backdrop against which changes in the modern faunas and ecosystems can be evaluated (e.g., Cohen et al. 2007, 2013; Verschuren et al. 2002). Apart from the almost continuous faunal data that can be retrieved from lake coring, several basins contain abundant outcrops with rich macrofossil assemblages. Collectively, the outcrops in some basins likewise provide exceptional temporal resolutions (Van Bocxlaer et al. 2012a, Williamson 1981), and in a number of cases they contain direct ancestors of species and clades existing today (Van Bocxlaer & Hunt 2013).

Limited information on the patterns and processes of morphological change in AGL biota is available, and as a result we are still in the early days of the study of macroevolution. One exception was Williamson's (1981) claim that fossil molluscs from the Turkana Basin present *prima facie* evidence for punctuated equilibrium (Eldredge & Gould 1972). Longer periods of limited morphological change are indeed interrupted by short intervals of marked change in morphology, but the latter are caused by biological invasions of unrelated taxa rather than ancestor-descendant change (Van Bocxlaer et al. 2008). A quantitative analysis of stasis versus gradual change within Turkana Basin molluscs remains lacking. To our knowledge, only one case of AGL biota has been analyzed quantitatively, i.e., an ongoing gastropod radiation from Lake Malawi, and all morphological traits studied displayed morphological stasis (Van Bocxlaer & Hunt 2013). More evidence for punctuated equilibria in AGL molluscs may exist (e.g., Van Damme & Pickford 1999, 2003), and the combination of long periods of morphological stasis within species lineages and rapid morphological changes coinciding with lineage splitting may be the representation of evolutionary (adaptive) radiations in the fossil record.

Paleontological data (Van Bocxlaer et al. 2008, Van Damme & Pickford 2003) also suggest that species sorting or species selection has occurred in the AGL. Many of the differences in species richness between clades, and hence the emergent propensity of clades of AGL biotas to diversify, are caused by interactions between intrinsic biological traits and the environment. In some cases these biological traits may well reside at the organismic or species level. For example, intrinsic biological traits, e.g., brooding, can affect the geographic range and life history of species, and the maintenance of small geographic ranges and population sizes may contribute to reproductive isolation and cladogenesis, as appears to have been the case for the species flock of *Lavigeria* gastropods from Lake Tanganyika (Michel et al. 2004).

ECOSYSTEM AND BIODIVERSITY CONSERVATION

The remarkable ecosystems and biodiversity of the AGL currently face numerous anthropogenic threats, ranging from activities within their watersheds to global climate change. The AGL ecosystems are not as widely known as popular ecotourism destinations such as the Galápagos Islands, the Hawaiian Islands, and tropical reefs, and this has probably contributed to a more limited attention to address the problems of species extinction and widespread habitat alteration that are ongoing in these lakes, despite the marked changes that have been documented already (Cohen et al. 2005, McIntyre et al. 2005, Verschuren et al. 2002). Species introductions and subsequent ecosystem collapse are probably the most widely reported impacts (especially regarding the introduction of Nile perch into Lake Victoria; Barel et al. 1985; Hecky et al. 2010; Witte et al. 1992, 2013), though many other sources of ecosystem disturbance exist. For example, increased human population growth, land use, and the rapid expansion of fertilizers in the late twentieth century have resulted in increased turbidity and rapidly changing algal communities (Hecky 1993, Otu et al. 2011, Verschuren et al. 2002). Turbidity has affected visual predation and mate recognition systems in cichlids up to the point that selective mating could not be maintained, leading to hybridization (Seehausen et al. 1997).

Punctuated equilibrium:

the theory that fossil species lineages undergo little morphological change over long periods (stasis) except for rapid morphological change (punctuations) at lineage splitting

Species selection:

the selection on species traits (e.g., geographic range) similar to how individual traits (e.g., body size) act as units of selection in natural selection

Deforestation and watershed erosion are other factors that altered the sensitive littoral zone, particularly through high sedimentation rates, changed substrate composition, a subsequent loss of biodiversity, and altered species interactions (Alin et al. 1999, Cohen et al. 2005, Eggermont & Verschuren 2003, McIntyre et al. 2005). Most recently, intense exploration of hydrocarbons in the AGL has begun. Discovery wells near Lake Albert have already been developed, and intensive exploration is also under way in the Turkana Basin and at Lake Tanganyika. Beyond these indirect effects through ecosystem interactions, unsustainable resource exploitation (e.g., use of fishing nets with fine mesh sizes) has exhausted fish stocks directly (Lowe-McConnell 1993). The significance of these developments is moreover increased by the division of most AGL by national boundaries, and economic instability has hampered the development of transnational agreements, such that lake management and conservation infrastructure remain weak. Perhaps of even greater concern is the initially slower but increasing impact of global climate change, which is largely beyond the control of local authorities. The surface waters of at least some of the meromictic AGL are warming, which strengthens stratification and hence reduces the depth of oxygenation and the nutrient influx from deep waters to the epilimnion. This warming has changed primary productivity and the interactions between the pelagic and benthic ecosystems, and it has resulted in a loss of benthic habitat and diversity (Eggermont & Verschuren 2003, O'Reilly et al. 2003, Tierney et al. 2010, Van Bocxlaer et al. 2012b). Given the fragile limnological balance on which the extraordinary biodiversity of the AGL depends, much more ecosystem monitoring and conservation strategies are needed to preserve the AGL biota and the varied ecosystem services and resources that these fascinating ecosystems provide to society.

SUMMARY POINTS

1. The AGL are one of the most remarkable freshwater features on our planet, and their extraordinary ecosystems incorporate some of the most diverse and renowned radiations of freshwater biotas on earth. Marked differences in basin formation, tectonic activity, and climate regimes between basins have shaped the ecosystem characteristics and faunas of each lake differently.
2. The AGL are quasi eco-insular systems, and like oceanic islands, most of their biodiversity has evolved through evolutionary (adaptive) radiations, in which both ecological opportunity and intrinsic biological factors have played prominent roles. In addition to remarkable endemism, great morphological disparity is observed, and it is often strongly correlated with niche diversity.
3. In this phenomenal setting of quasi-replicate lake systems, much iterative evolution and morphological convergence are observed between and within lake basins.
4. The biodiversity of the AGL depends heavily on a delicate limnological balance and overall ecosystem stability: Larger and deeper lakes have a greater buffering capacity and more diverse species assemblages. In the more stable lakes, complex ecological interactions such as coevolution (e.g., predatory-prey arms race) and ecosystem engineering are noteworthy consequences.
5. Taxa of the more stable lakes often show remarkable phylogenetic structure related to past cycles of lake-level change. Other lakes that have undergone more ecosystem calamities harbor more species that are widespread and fewer species flocks that evolved within the lake (less endemism).

6. The diversity and morphological disparity of clades within the AGL have waxed and waned through time. Some fossil faunas demonstrate morphological stasis and conform to punctuated equilibria, but gradual changes have been observed as well. Species selection appears to have shaped differences in species richness in clades of AGL biotas.
7. The remarkable ecosystems and biodiversity of the AGL currently face numerous anthropogenic threats, both directly through unsustainable resource use and indirectly through human activities within these lakes' watersheds and beyond (e.g., global warming). Much more ecosystem monitoring and conservation actions are needed to preserve the AGL biotas and to make our demands on these fascinating ecosystems more sustainable.

FUTURE ISSUES

1. Evolutionary biology is in part an inductive science in which generalities are established by the accumulation and comparison of case studies, and very few adaptive radiations have been studied extensively. Documenting the adaptive nature of radiations in AGL biotas other than cichlids through a variety of approaches and disciplines is urgently needed.
2. Our review indicates that vertebrates and invertebrates of the AGL share a number of evolutionary patterns, but that differences exist as well. More work is needed, especially on invertebrates, so that the comparison of evolutionary ecology and diversification dynamics across the tree of life becomes feasible.
3. With the advent of next-generation DNA and RNA sequencing technologies, it is now possible to scrutinize the evolution of entire genomes and of gene regulatory pathways in the context of speciation and adaptive radiation. We strongly recommend applying these novel approaches to the faunas of the AGL, which would undoubtedly improve our understanding of the molecular and biophysical bases of organismal diversification.
4. More paleontological work is required to document patterns of evolution in the AGL, in part because the exceptional resolution of rich fossil archives in the East African Rift provides an important means of bridging micro- and macroevolution and uniting the fields of evolutionary biology and paleontology.
5. The development of molecular paleobiology, i.e., the molecular study of fossil DNA, would allow the construction of molecular phylogenies for superbly preserved fossils from lake sediments. The combination of molecular and morphological data sets spanning from stem to crown members of lacustrine radiations, all within the context of a well-documented environmental history, offers a truly exciting prospect for the study of evolutionary dynamics and adaptive radiation.
6. The compilation of continent-wide data sets would allow the study of macroevolutionary and macroecological patterns, such as latitudinal diversity gradients, and their underlying causes.
7. More long-term ecosystem data and biodiversity monitoring related to ongoing threats to the AGL are required to inform conservation policy and decision making.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank Kaustuv Roy for the opportunity to write this review and for input on an earlier draft; Craig Feibel, Michael McGlue, Ellinor Michel, Peter Reinthal, Chris Scholz, and Jos Snoeks for input on **Figures 1** and **2**; and Dirk Verschuren and Gene Hunt for insightful comments on an earlier draft. W.S. was supported by the European Research Council (StG ‘INTERGENADAPT’; CoG ‘CICHLID~X’) and the Swiss National Science Foundation (grants 3100A0_138224 and CRSII3_136293). B.V.B. was supported by a Peter Buck Fellowship of the Smithsonian Institution, an Alexander von Humboldt Fellowship, and the Flanders Research Foundation. A.S.C. was supported by NSF grants EAR 9510033, 9619458, 0223920, and 0602350, and the UNDP/GEF-Lake Tanganyika Biodiversity Project. W.S. and B.V.B. contributed equally to this manuscript.

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