Recent ecological change in ancient lakes

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Abstract

Ancient lakes are among the best archivists of past environmental change, having experienced more than one full glacial cycle, a wide range of climatic conditions, tectonic events, and long association with human settlements. These lakes not only record long histories of environmental variation and human activity in their sediments, but also harbor very high levels of biodiversity and endemism. Yet, ancient lakes are faced with a familiar suite of anthropogenic threats, which may degrade the unusual properties that make them especially valuable to science and society. In all ancient lakes for which data exist, significant warming of surface waters has occurred, with a broad range of consequences. Eutrophication threatens both native species assemblages and regional economies reliant on clean surface water, fisheries, and tourism. Where sewage contributes nutrients and heavy metals, one can anticipate the occurrence of less understood emerging contaminants, such as pharmaceuticals, personal care products, and microplastics that negatively affect lake biota and water quality. Human populations continue to increase in most of the ancient lakes' watersheds, which will exacerbate these concerns. Further, human alterations of hydrology, including those produced through climate change, have altered lake levels. Co-occurring with these impacts have been intentional and unintentional species introductions, altering biodiversity. Given that the distinctive character of each ancient lake is strongly linked to age, there may be few options to remediate losses of species or other ecosystem damage associated with modern ecological change, heightening the imperative for understanding these systems.

Ancient lakes occupy a unique intersection of ecological and human heritage. While most lakes are < 10,000 yr old, a small proportion are much older, having formed more than 100,000 yr ago. Over their long histories, these sites have persisted through multiple cycles of warming and cooling, wet and dry periods, and substantial changes in both biology and physico-chemical conditions. At the same time, ancient lakes have supported some of the earliest known human settlements and played a key role in human cultural evolution and development (e.g., Nomokonova et al. 2010). Today, despite covering < 1% of land surface area, ancient lakes contain nearly half of the world's unfrozen fresh surface water, and a disproportionate share of the world's freshwater biodiversity (Dudgeon et al. 2006). Ancient lakes also support major economies, including tourism and fisheries, and face a suite of

Box 1: Definition of an ancient lake
Here, we define an "ancient lake" as one that has existed for at least one glacial cycle, i.e., was present at or before 130 ka BP (Lisiecki and Raymo 2005; Albrecht and Wilke 2008; Cheng et al. 2009). This criterion spans the last interglacial period, Marine Isotope Stage 5e (116–130 ka BP; Shackleton et al. 2003; Lisiecki and Raymo 2005) which has been used as a reference point for climate change (Yin and Berger 2015). This criterion also corresponds to an inflection point in the global distribution of lake ages, excluding the vast majority of which are < 10,000 yr old. We recognize that more liberal or conservative criteria could be argued, but the decision is ultimately subjective and somewhat secondary to our goals in this article. By focusing on lakes that are > 130,000 yr old, we have emphasized lakes that are in the far upper end of the distribution for age and are undeniably very old relative to the majority of lakes on the planet.

Box 2: The Baikal seal
Lake Baikal is home to the world's only exclusively freshwater seal, the nerpa (*Pusa sibirica*, the Baikal seal). Early explorers and Russian settlers arriving to the Baikal region in the 17th and 18th centuries recorded that the indigenous Buryat people inhabiting the region used nerpa as a source of furs, meat and fat. As human population in the catchment increased, so did the demand and the hunt for nerpa: the furs became an important commodity and nerpa blubber was commercially processed for use in the leather- and soap-making industries and for lighting. Irregularly enforced regulations throughout the early and mid-20th century created fluctuation in harvest counts, with steep declines in the 1930s and early 1940s. Harvests peaked in the 1980s, when the annual quota was set at 6000 individuals, declining to vary between 1000 and 2000 individuals/yr over the last decade, with quotas ranging between 600 and 3500 individuals (Petrov 2009; MNRERF 2014; Fig. 8b). However, in 1987/1988, morbillivirus infections led to the die-off of thousands of nerpa (Grachev et al. 1989). Commercial hunting has been prohibited since 2007, with harvest allowed only as a sustenance fishery for the native people of Siberia and for scientific and research purposes (MNRERF 2014). Relatively little information exists about the status of the nerpa population in Baikal through time compared to information about harvests. Systematic surveys begun in the 1970s and population numbers have varied between 68,000 and 120,000 since then (Fig. 8b, Pastukhov 1993; Petrov 2009). Currently, the population appears to be thriving, with the most recent estimate (2014) of 114,400 individuals (MNRERF 2014). Photo: Kantor/Greenpeace.

Fig. 1. Locations of ancient lakes in this review.

influences that have the potential to degrade their ecological, socio-economic, and scientific values. With unprecedented threats converging upon ancient lakes, a comprehensive understanding of their history, current status, and trajectory is needed in order to safeguard these systems for future scientific and societal benefit.

Ancient lakes serve a critical role as natural laboratories for research on speciation (Cristescu et al. 2010), paleohistory (Fritz et al. 2010; Lyons et al. 2015; Wilke et al. 2016), and limnology. While there have been decades of limnological research on individual ancient lakes such as Baikal, Victoria, Tanganyika, and the Aral Sea, comparative ecological studies of ancient lakes as a broader group are rare. Available knowledge about ancient lakes indicates they are biodiversity hot spots (Rossiter and Kawanabe 2000; Kostoski et al. 2010) that possess many species found nowhere else on the Earth (Albrecht and Wilke 2008), including monophyletic groups of closely related species (Cristescu et al. 2010) that, in turn, may share similar vulnerabilities. This high endemism occurring in monophyletic groups suggests that ancient lakes should be more susceptible to large ecological changes than geologically younger lakes, lending urgency to our work. Cristescu et al. (2010) predict that "after a drastic ecological perturbation, an ancient lake would be less resistant to invasions with a high probability of new niches being made available." Integrated research on the similarities and differences among ancient lakes, and their anthropogenic influences, would be valuable to limnology and ecology, and could guide management prioritization in these cherished ecosystems.

Several common categories of anthropogenic change are underway across lakes globally, inclusive of ancient lakes. Such changes include alterations of nutrient cycles (Moss 2012), pollution (Carpenter et al. 1998; Telmer et al. 2006; Eerkes-Medrano et al. 2015), temperature and stratification dynamics (O'Reilly et al. 2003, 2015), hypoxia (North et al. 2014; Jenny et al. 2016), lake level (Micklin 2007), food web structure including impacts of non-native species (Vander Zanden et al. 1999), as well as the abundance and phenology of ecologically or socioeconomically important organisms (Johnk et al. 2008; Thackeray et al. 2013; Francis et al. 2014). The intent of this review is to evaluate major anthropogenic threats faced by these unique ecosystems and the ecological changes that have already been documented. In doing so, we hope to encourage future comparative ecological studies across ancient lakes worldwide. Here, we define ancient lakes as those that have experienced one full glacial cycle (lakes older than 130 ka BP, *see* Box 1), recognizing that other definitions could be supported.

We focus our review on 29 ancient lakes (Figs. 1, 2; Table 1). These lakes include both hydrologically open (exorheic) and closed (endorheic) systems, and more than half of the lakes are very large (surface area > 500 km^2) (Fig. 3b). The lakes are globally distributed across latitudes, and over a spectrum of catchment land uses and regional socio-economic conditions. In addition, the shorelines and catchments of these lakes often cross geopolitical boundaries. For example, the shoreline of the Caspian Sea is shared by five countries (Russia, Kazakhstan, Turkmenistan, Iran, and Azerbaijan). Some of the ancient lakes discussed here are UNESCO World Heritage sites (Lakes Ohrid, Baikal, Inle), many have a long history of human settlement linked to subsistence fishing, and
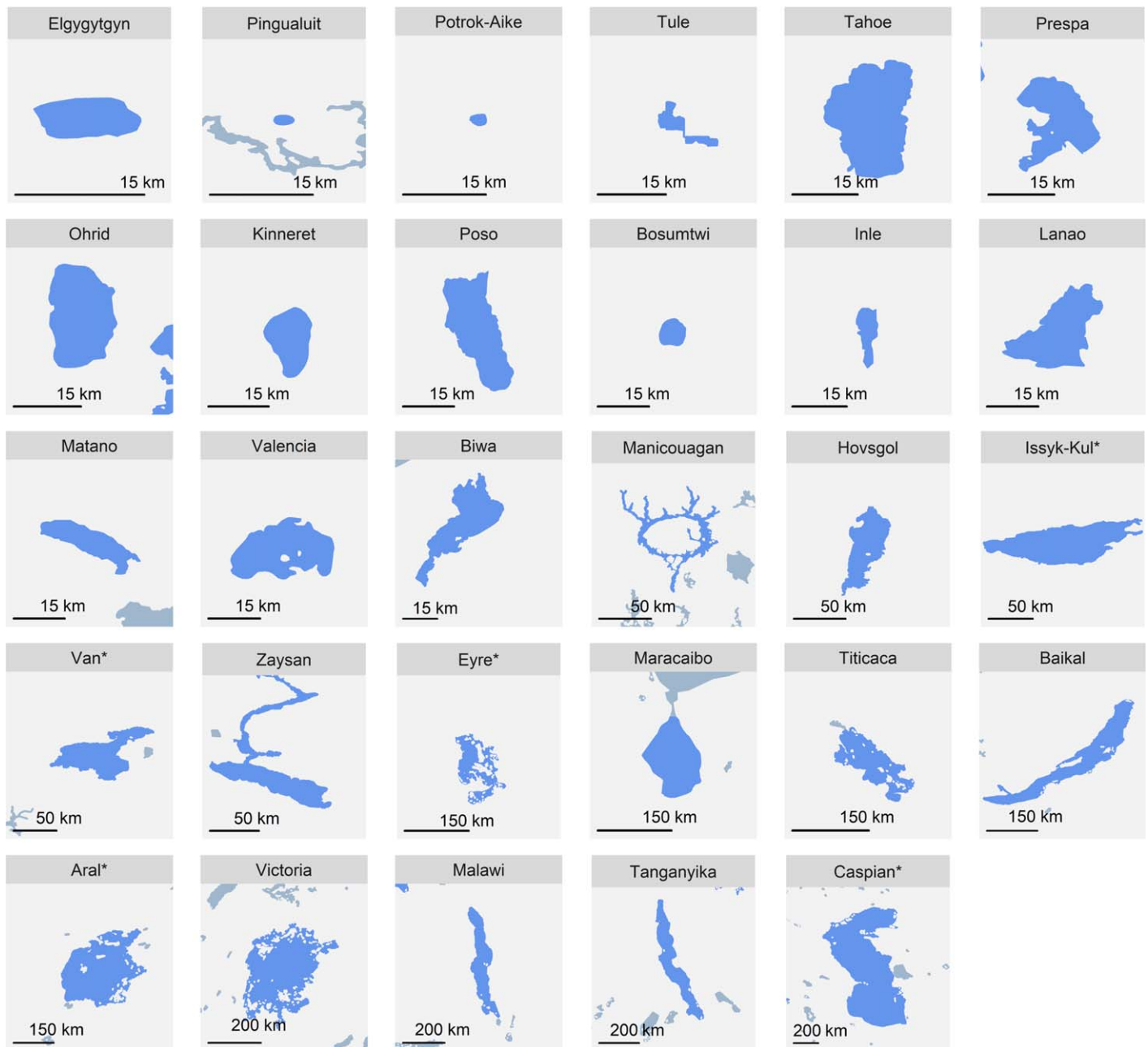
Fig. 2. Lake outlines of the ancient lakes in this review in blue, surrounding water bodies in gray. Asterisk (*) indicates a saline lake. Lake polygons were obtained from the Global Lakes and Wetlands Database-Level 2 (GLWD, Lehner and Doell 2004). A small number of lakes not present in GLWD (Eyre, Pingualuit, Potrok-Aike, Tule) were obtained from the Hydrolakes database (Messager et al. 2016). Lake Maracaibo was added manually.

others such as Lake Tahoe support major tourism industries (Nechodom et al. 2000 in Raumann and Cablk 2008). Our review includes climate change in the context of these ancient lakes' longer climatological histories; problems of water quality, including nutrient enrichment from urban and agricultural development and atmospheric deposition; invasive species; other pollutants, including metals and plastics; water extraction and hydrologic modification; and resource exploitation. Many of these factors are interconnected and co-occurring within individual lakes, with outcomes mediated by the lake morphology and hydrology, and we attempt to highlight such interconnections with case examples when appropriate.

Climatological history

Ancient lakes have a long history of exposure to a changing environment, with significant fluctuations in air temperatures and precipitation over glacial-interglacial cycles. A substantial

Table 1. Physiographic information for the 29 ancient lakes in this review. For impact crater lakes, we used the time since impact.

Lake name	Code	Lat. (°)	Long. (°)	Region	Country	Form	Approx. age (Ma)
Aral Sea	ARAL	45.1605	58.5265	Middle East	Kazakhstan/ Uzbekistan	Tectonic depression	>5
Lake Baikal	BAIK	53.5000	108.0000	Siberia	Russia	Tectonic graben	>25
Lake Biwa	BIWA	35.3333	136.1667	South Pacific	Japan	Tectonic half graben	0.43
Lake Bosumtwi	BOSU	6.5050	−1.4083	Africa	Ghana	Impact crater	1.07
Caspian Sea	CASP	41.6667	50.6667	Middle East	Kazakhstan/Russia/ Azerbaijan/Iran/ Turkmenistan	Tectonic depression	>5
Lake El'gygytgyn	ELGY	67.4909	172.0868	Siberia	Russia	Impact crater	3.6
Lake Eyre	EYRE	−28.3667	137.3667	South Pacific	Australia	Depression	>0.13
Lake Hovsgol (Khuvsgul)	HOVS	51.1000	100.5000	Middle Asia	Mongolia	Tectonic graben	2–20
Lake Inle	INLE	20.5500	96.9167	South Asia	Myanmar (Burma)	Tectonic graben	1.5
Lake Issyk-Kul	ISSY	42.4167	77.2500	Middle East	Kyrgyzstan	Tectonic graben	>3
Lake Kinneret (Sea of Galilee)	KINN	32.8333	35.5833	Middle East	Israel	Tectonic graben	Uncertain
Lake Lanao	LANA	7.8811	124.2631	South Asia	Philippines	Volcanic collapse	0.01–10
Lake Malawi (Nyasa, Niassa)	MALA	−12.1833	34.3667	East African Rift	Malawi/Mozambique/ Tanzania	Tectonic half graben	3.6–5.5
Manicouagan Reservoir	MANI	51.2722	−68.3265	North America	Canada	Impact crater	214
Lake Maracaibo	MARA	9.8158	−71.5567	South America	Venezuela	Tectonic uplift	>20
Lake Matano	MATA	−2.4853	121.3330	South Pacific	Indonesia	Tectonic graben	1–2
Lake Ohrid	OHRI	41.0000	20.7500	Balkans	Macedonia/Albania	Tectonic graben	2–5
Lake Pingualuit	PING	61.2750	−73.6603	North America	Canada	Impact crater	1.4
Lake Poso	POSO	−1.9244	120.6167	South Pacific	Indonesia	Tectonic	2
Lake Potrok-Aike	POTR	−51.9631	−70.3794	South America	Argentina	Volcanic maar	0.77
Lake Prespa	PRES	40.9000	21.0333	Balkans	Albania/Greece/ Macedonia	Tectonic graben	2–5
Lake Tahoe	TAHO	39.0917	−120.0417	North America	USA	Tectonic half-graben	2
Lake Tanganyika	TANG	−6.5000	29.8333	East African Rift	Tanzania/DR Congo/ Burundi/Zambia	Tectonic half graben	<9–12
Lake Titicaca	TITI	−15.7500	−69.4167	Andes	Peru/Bolivia	Tectonic uplifted plain	<3
Lake Tule	TULE	41.9013	−121.5250	North America	USA	Displacement basin	>3
Lake Valencia	VALE	10.1939	−67.7316	South America	Venezuela	Tectonic graben	2–3
Lake Van	VANL	38.6333	42.8167	Middle East	Turkey	Tectonic depression	>0.5
Lake Victoria	VICT	−1.0000	33.0000	Africa	Kenya/Uganda/Tanzania	Tectonic uplift	<0.8
Lake Zaysan	ZAYS	48.0000	84.0000	Middle East	Kazakhstan	Tectonic depression	>65

number of extant ancient lakes date back to the Pliocene (5.3–2.6 Ma) (*see* Pound et al. 2014), a period marked by globally warmer and wetter conditions, which peaked in the Piacenzian (late Pliocene: 3.6–2.6 Ma), with global mean temperatures 2–3°C warmer than present (Salzmann et al. 2011). Evidence of abrupt environmental change is captured in lake sediments dating back to the Pliocene (Weber et al. 2010), when surface Arctic temperatures may have exceeded modern values by as much as 19°C (Ballantyne et al. 2010; Csank et al. 2011a,b). During the last interglacial period (MIS 5e), high-latitude temperatures

peaked at 2–8°C above those of the 20th century (NGRIP—North Greenland Ice Core Project members 2004; CAPE-Last Interglacial Project Members 2006; Masson-Delmotte et al. 2011; Sánchez Goñi et al. 2012; NEEM community members 2013), while the last glacial maximum (LGM) averaged 8–10°C and in some locations > 17°C cooler than the Holocene (Braconnot et al. 2007; Shakun and Carlson 2010; Braconnot et al. 2012). Additionally, ancient lakes have been subjected to abrupt decadal and centennial climate changes (e.g., Fritz et al. 2010; Stager et al. 2011) linked to Heinrich and Dansgaard–Oeschger
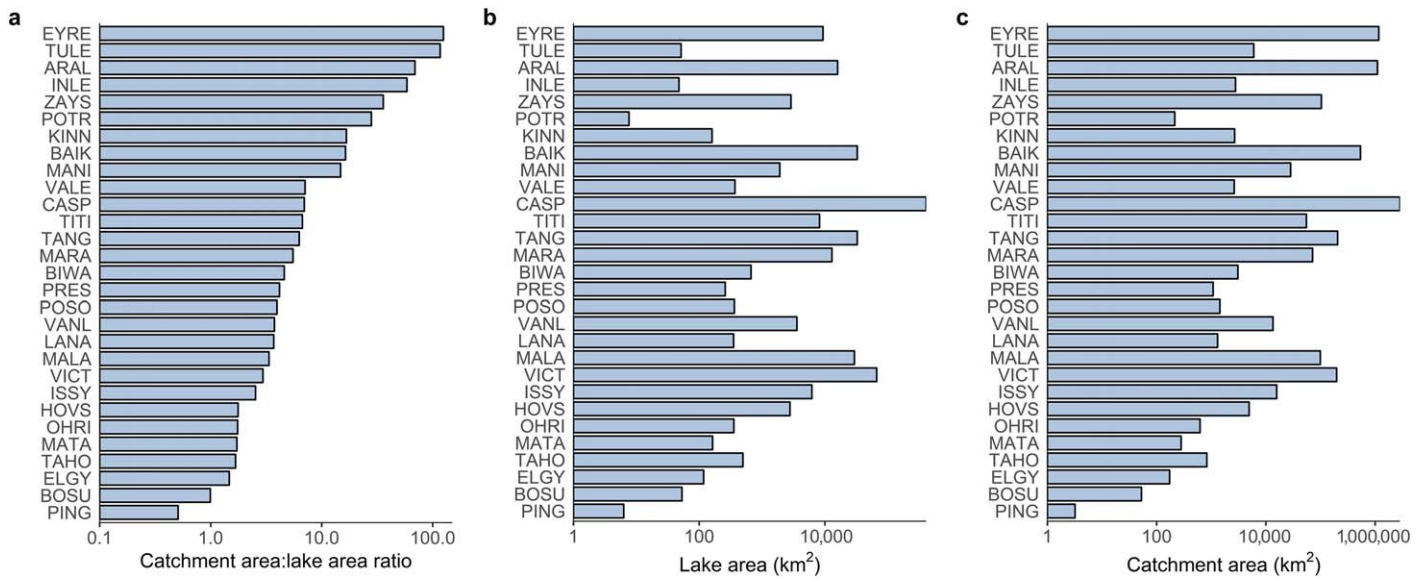
Fig. 3. (**a**) Catchment area : lake area ratio for each lake. (**b**) Lake area, in square kilometers. (**c**) Catchment area in square kilometers. Note log scale on *x* axes (*see* Table 1 for lake abbreviations).

Table 2. Warming rates for lakes with available long-term data. Warming rates reported for summer (JAS/JFM) surface temperatures (SSTs) in units of degree celsius/decade from O'Reilly et al. (2015) unless otherwise specified. Lake Biwa value is an annual average degrees/decade extrapolated from annual average degrees/year from Hsieh et al. (2010); Lake Baikal value is summer average from Hampton et al. (2008); and the Aral Sea value is summer average degrees/decade extrapolated from May average degrees/year from Ginzburg et al. (2003).

Lake name	SST warming Satellite	SST warming in situ
Aral Sea	1.1	—
Caspian Sea	0.75	—
Lake Baikal	0.68	0.03
Lake Baikal	—	0.2
Lake Biwa	—	0.28
Lake Hovsgol (Khuvsgul)	0.27	—
Lake Issyk-Kul	0.29	—
Lake Kinneret (Sea of Galilee)	—	0.44
Lake Malawi (Nyaya, Niassa)	0.11	—
Lake Tahoe	0.71	0.54
Lake Tanganyika	0.19	0.14
Lake Titicaca	0.15	—
Lake Van	0.28	—
Lake Victoria	0.3	—
Lake Zaysan	0.25	—

events (Hemming 2004; Capron et al. 2010) including the last glacial-interglacial transition (LGIT) (Clark et al. 2012).

One direct response of high- and mid-latitude ancient lakes (i.e., those above 50° latitudes) to climatological changes is change in ice cover, thickness, and duration. Interesting cases include Lake Baikal (Siberia) and Lake El'gygytgyn (Arctic North East Siberia) which, despite their high latitudes, were never glaciated (Grosswald and Kuhle 1994; Brigham-Grette et al. 2013). Lower latitude systems were more strongly influenced by changes in precipitation, evaporation, and tributary inflows. For example, Lake Victoria (East Africa) may have dried out during parts of the LGIT due to reductions in precipitation (Stager et al. 2011), and lake level in many ancient lakes has changed hundreds of meters during the quaternary (< 2.6 Ma) as a result of altered precipitation patterns (D'Agostino et al. 2002; Scholz et al. 2007). The combination of these climatological changes, together with their associated impact on inputs of allochthonous material and nutrients, physical limnology, and biogeochemical cycling, has produced massive changes in ecosystem structure and the extinction and evolution of taxa (e.g., Mackay et al. 2010).

Modern climate change effects on ancient lakes

Ancient lakes are susceptible to ongoing shifts in climate, which can involve changes in the central tendency and variability of water temperature, water levels, mixing, and other fundamental physical properties. In the 15 ancient lakes for which data exist, warming has occurred (Table 2). The warming ranged from 0.11°C per decade in Lake Malawi to 0.75°C per decade in the Caspian Sea (Ginzburg et al. 2003; Hampton et al. 2008; Hsieh et al. 2010; O'Reilly et al. 2015; Sharma et al. 2015). These warming trends in ancient lakes parallel a broader pattern across 235 lakes worldwide, which has shown a mean increase of 0.34°C per decade since 1985 (O'Reilly et al. 2015). In the case of tropical Lake Tanganyika, a 0.13°C per decade

warming trend has influenced the dynamics of thermal stratification (O'Reilly et al. 2003; Kraemer et al. 2015). Similarly, Lake Ohrid has experienced decreased vertical mixing as temperatures have warmed (Matzinger et al. 2007). In subarctic Lake Baikal (Todd and Mackay 2003) and the temperate Caspian Sea (Kouraev et al. 2004), lake ice duration and extent have declined over the past century, as it has in other lakes that freeze (Magnuson et al. 2000). Surface waters in Baikal have warmed 0.20°C per decade since 1946 (Hampton et al. 2008).

The warming of these lakes has a variety of ecological consequences. While we can infer that climate change is already affecting many of the ancient lakes, currently information is sparse for many sites (Supporting Information Table S4). Baikal's warming temperatures in the summer are associated with increasing chlorophyll and greater presence of cosmopolitan species relative to the endemic, cold-loving zooplankton (Hampton et al. 2008; Izmest'eva et al. 2016). In contrast, increased thermal stratification associated with warming in Lake Tanganyika has caused decreases in productivity and declines in biomass throughout the food web (O'Reilly et al. 2003; Verburg et al. 2003; Cohen et al. 2016), and similar trends are likely in other permanently stratified lakes such as Lake Malawi. In Lake Biwa, warmer winters have altered dominant winter phytoplankton and subsequently the ability of certain zooplankton to overwinter (Tsugeki et al. 2009). Based on studies in geologically younger lakes, warming is likely to have cascading effects in food webs (Adrian et al. 2009), including but not restricted to altering plankton and fish phenology (Weyhenmeyer et al. 1999; Adrian et al. 2006; Thackeray et al. 2010), organism body size (Moore et al. 1996), harmful algal blooms (Paerl and Huisman 2009), and ecosystem-level greenhouse gas emissions (Ducharme-Riel et al. 2015). Even relatively small changes in temperature may shift food webs and ecosystem functioning in these lakes as waters warm. For warm tropical lakes, organisms may already be living close to physiological maxima (Tewksbury et al. 2008) and due to physical properties of water, relatively small changes in temperature can dramatically reinforce stratification (O'Reilly et al. 2003). In coldwater lakes, Moore et al. (2009) posit that biotic communities dominated by coldwater stenotherms may be steadily outcompeted by cosmopolitan species as waters warm.

Climate change may also alter terrestrial–aquatic linkages, e.g., through shifts in fire regime, as documented in the charcoal content of ancient lake sediments (Tierney et al. 2010). A recent surge in fire activity has raised concerns worldwide (e.g., Bowman et al. 2009), yet the implications for surface waters remain uncertain. Fire is known to increase, and otherwise alter the characteristics of watershed loading of sediment, nutrients, and pollutants, with effects that linger for at least several years (Smith et al. 2011). The specifics of these changes depend upon characteristics of not only the lake but also the watershed and the fire itself.

Unfortunately, long-term limnological records are not available for most of the ancient lakes, and the impacts of climate change are also often confounded by local anthropogenic change, such as eutrophication at Lake Biwa (Hsieh et al. 2011), Valencia, and elsewhere. As lakes continue to warm with rising air temperatures (Schmid et al. 2014), in concert with altered global patterns of solar radiation and cloud cover (O'Reilly et al. 2015), we can anticipate a wide variety of both direct and indirect ecological consequences.

Lake level changes

Many of the world's ancient lakes have undergone large fluctuations in lake level (Supporting Information Table S4), driven by both human modification of hydrology and climate variation. As early as the 1800s, the naturalist Alexander von Humboldt noted that watershed deforestation and irrigation were associated with Lake Valencia's falling water level (Wulf 2016). Dams for storage and hydropower have further altered lake levels with varying impact. Major hydropower projects exist at the outflows of Baikal, Victoria, Lanao, Manicougan, and Zaysan, and water levels have been raised considerably by dams in the latter two lakes. In contrast, Ohrid, Kinneret, Biwa, Titicaca, and Tahoe have smaller outflow regulation structures. Such anthropogenic changes are embedded within background cycles of climate-driven lake-level changes. During the 19th century, both the highs and lows of many of the African Great Lakes were more extreme than those of the 20th century (Nicholson 1998). Tropical Lake Titicaca in South America has fluctuated ∼ 7 m in level during the last century, with massive flooding of agricultural fields surrounding the lake during years of unusually high rainfall, and consequent impacts on the local economy (Pawley et al. 2001). In some high-latitude regions, changes in hydrology associated with warming have increased the duration of the ice-free season and inflow via snow melt affecting hydrologic mass balances. In Lake Baikal, e.g., river inflow has increased significantly over the last century, associated with increased air temperatures and precipitation (Moore et al. 2009).

Ancient lakes found in regions with low precipitation and runoff to evaporation ratios (Cohen 2012) may exhibit the most extreme hydrological changes. Serious negative consequences of altered hydrologic patterns have occurred in climate-sensitive, impoverished regions that are unable to make large technological investments to deal with changing surface flows and lake levels (Vörösmarty et al. 2010). The most dramatic examples involve water extraction for either agriculture or urban use, as exemplified by the notorious case of the Aral Sea, once the fourth largest lake in the world by area and presently nearly dry (see below).

Less dramatic anthropogenic water level declines may still have major impacts on communities reliant on ancient lakes for a variety of ecosystem services. Declines in the level of
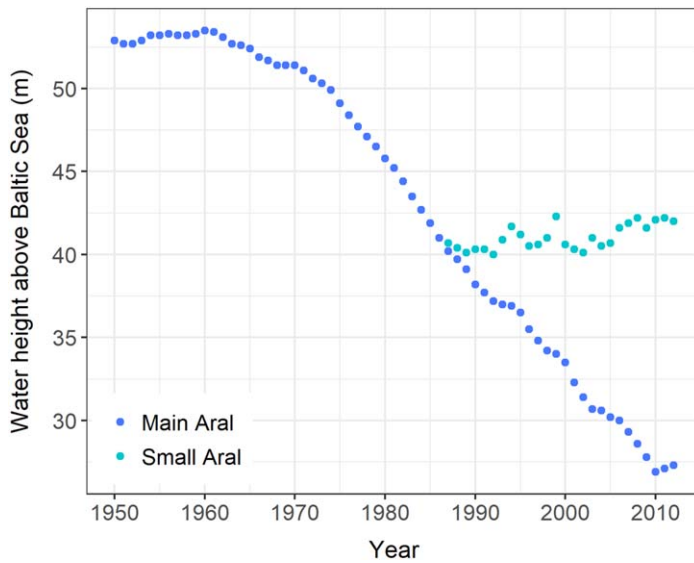
Fig. 4. Long-term water level changes in the Aral Sea. As the lake level dropped, two distinct basins emerged (small and main). Data are from Cretaux et al. (2013) which used a combination of in situ measurements and satellite altimetry, with additional data from Cretaux (pers. comm).

Lake Victoria, e.g., appear to be more strongly influenced by increased water use in the catchment than by climate variability, creating conflict over water resources during the last decade (Awange et al. 2008). An increase, rather than decrease, in water level can be equally problematic: at Lake Van, natural water level increases have damaging consequences for surrounding infrastructure (Deniz and Yildiz 2007). Water regulation through dam construction has also altered ancient lake hydrology in recent decades. An increase in water level of $\sim$ 1 m in Lake Baikal was caused by hydroelectric power reservoir construction in the 1950s (Moore et al. 2009) and at Lake Zaysan, the installation of a series of dams in the 1960s resulted in a 6 m increase in water level (Bai et al. 2012). Although the magnitudes of these recent water level fluctuations are not necessarily unprecedented, they are affecting resource use by the surrounding human communities and occurring more rapidly than those associated with long-term climate cycles.

Returning to the iconic example of the Aral Sea, altered flow regimes have led to catastrophic environmental consequences. The Aral Sea is an endorheic lake in central Asia that first started to in-fill about 140,000 yr ago. Today, it sits within the countries of Kazakhstan and Uzbekistan, and the drainage basin of its two main rivers, the Amu Dar'ya and the Syr Dar'ya are vast, spanning some 1.8 million km^2 across six countries. The history of the Aral Sea has long been intertwined with ancient settlements going back thousands of years (Boroffka et al. 2006), and recurring reductions in water level have occurred over the past 5000 yr (Boroffka et al. 2006; Cretaux et al. 2013), linked to complex interactions between natural climate variability and human

action. This long history of anthropogenic impact may be the reason why even during periods of high-lake level (e.g., prior to 1960 A.D.), biodiversity was never as high as reported in other ancient lakes, although several indigenous species provided the basis for economically important fisheries (Micklin 2007).

Since the 1960s, Aral Sea has lost over 90% of its volume (Fig. 4) due to water diversion to irrigate 8 million hectares of desert sand for cultivation of cotton, or "white gold." Lake water levels dropped from a high of c. 55 m a.s.l. to under 30 m a.s.l., with many parts now dried out completely (Cretaux et al. 2013). The shrinkage of the Aral Sea represents the largest transformation of water to permanent land seen anywhere in the world over the past 30 yr (Pekel et al. 2016). Salinity increased from 10 g L^{-1} to $>$ 100 g L^{-1} (Micklin 2007). The impact has been so great that the Aral Sea has now contracted into multiple smaller water bodies further separated by marsh and desert (Fig. 4). Surprisingly, the Small Aral Sea (newly formed lake to the north) has seen its fishing economy and biodiversity return, as water levels rose with the building of dams to prevent water loss to the larger, more southern Large Aral (Micklin 2007). The impact of water loss from the Aral Sea has been devastating to local communities. Hundreds of thousands of people have been displaced, and exposure to toxic metals and agrochemicals of associated with bottom sediments has resulted in increased deaths and chronic disease (Kaneko et al. 2003). Ecosystems in and around the lake's pelagic region, Delta marshes, and fringing forests were decimated, and have experienced large-scale declines in biodiversity (e.g., Mirabdullayev et al. 2004; Micklin 2007). As the lake became hypersaline, most freshwater and brackish species declined, and the fishing industry died out in the 1980s.

Paleoclimatic changes in lake level often dwarf those of more recent history, particularly in closed-basin lakes in arid to semi-arid regions (e.g., Olaka et al. 2010). Lake Victoria, presently the world's largest tropical lake, desiccated during the late Pleistocene (Stager et al. 2011), and Lake Malawi and Lake Tanganyika, presently $>$ 700-m deep, dropped $>$ 500 m in level between 135 ka BP and 75 ka BP (Cohen et al. 2007; Scholz et al. 2007, Lyons et al. 2015). Similarly, Lake Titicaca was $\sim$ 85 m lower during the mid-Holocene ($\sim$ 6 ka), a time when humans were present in the basin, and $>$ 240 m lower during the last interglacial period, $\sim$ 125 ka (D'Agostino et al. 2002). The maximum level of Lake Kinneret occurred near the LGM $\sim$ 25 ka BP, when it rose $>$ 20 m and joined with Lake Lisan to the south, followed by intervals of lake-level decline of 10 m (Hazan et al. 2005). Even in large open lakes, such as Lake Baikal, Pleistocene lake levels were highly variable, controlled by a combination of both climatic and tectonic drivers (Colman 1998). For example, lake terraces show that during the middle Pleistocene (c. 200 ka BP), Lake Baikal water levels were up to 200 m higher than present, because tectonic activity altered drainage from the lake (Mats et al. 2000). During the
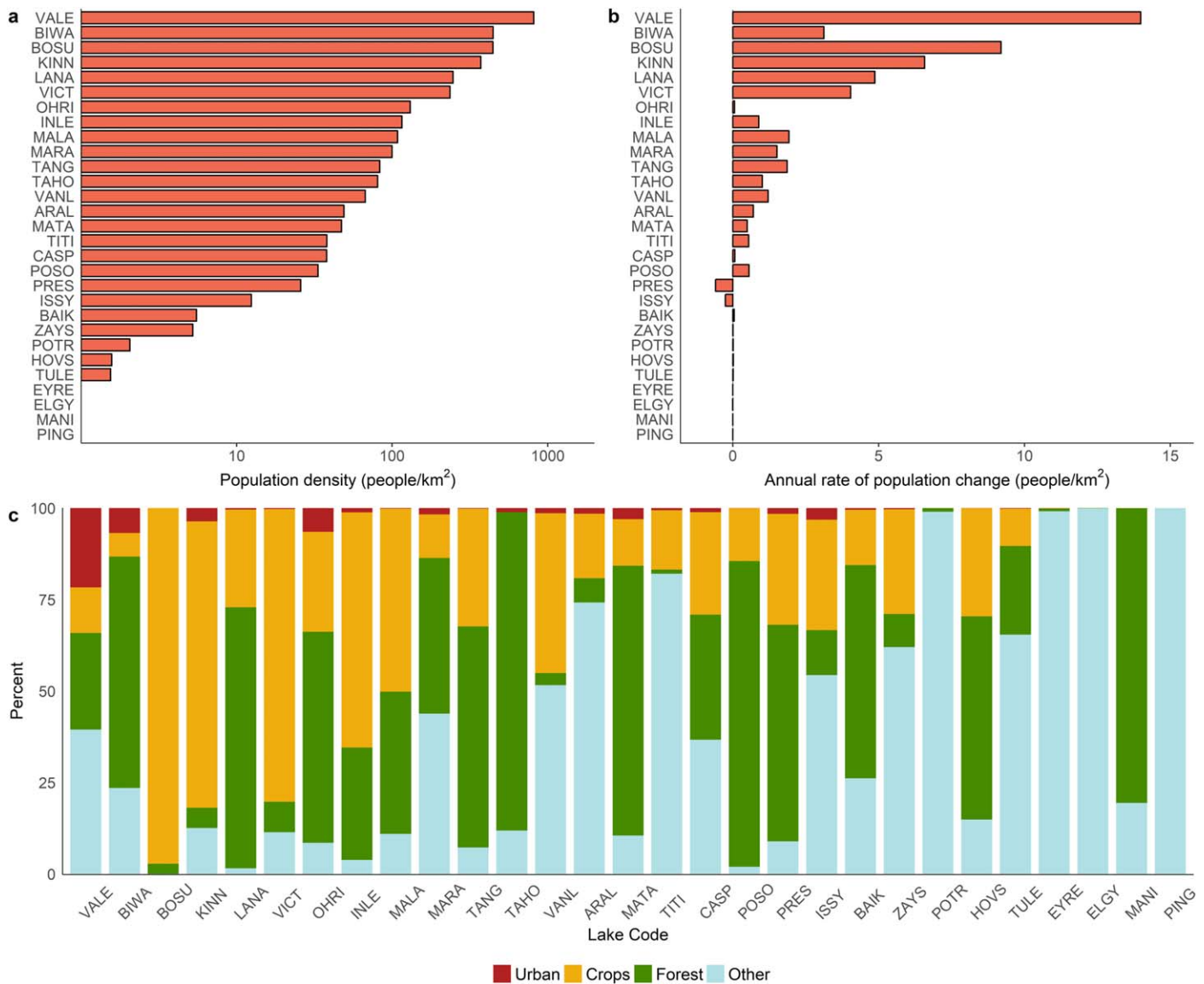
Fig. 5. (**a**) Population density in 2015 in people per km^2 of catchment. Note log scale on *x* axis. (**b**) Annual rate of population change (1990–2015). (**c**) Land use in 2010 in lake catchments. "Others" include grasslands, shrublands, and bare areas (*see* Supporting Information Table S3; *see* Table 1 for lake abbreviations).

LGM on the other hand, lake levels dropped by almost 40 m, linked to past climate, especially glacial runoff into the lake and increased evaporation rates (Osipov and Khlystov 2010).

Eutrophication: Sources and effects

Eutrophication is a serious threat to the ecological integrity of lakes worldwide (Carpenter et al. 1998). Increasing nutrient concentrations and the negative consequences of eutrophication have been recorded for most of the ancient lakes, including Victoria, Baikal, Valencia, Titicaca, and Ohrid among others (Supporting Information Table S4). The dominant sources of nutrient inputs to ancient lakes differ depending on

watershed land use and development, as do the severity and primary effects of eutrophication. One of the effects of eutrophication in ancient lakes is loss of biodiversity, given these systems' high rates of endemism. For example, in Lake Victoria, decreased water clarity has impacted reproduction by endemic cichlids, leading to the disappearance of dozens of species (Seehausen et al. 1997, 2003). In Lake Baikal, littoral algal blooms have recently been recognized as threatening the extraordinary diversity of the nearshore benthos (Timoshkin et al. 2016, 2018) and in Lake Tahoe, gradual decreases in water clarity appear to have precipitated declines of endemic deep-water macrophyte-invertebrate associations (Caires et al. 2013). In Lakes Valencia, Titicaca, and Victoria, pronounced

Fig. 6. Lake Valencia. Photo credit: NASA Earth Observatory, 27 October 2004.

eutrophication has caused harmful algal blooms and severe degradation of water quality for human use (Jaffé et al. 1993; Verschuren et al. 2002; ESA 2013). Effects of eutrophication are difficult to reverse in lakes, with idiosyncratic responses by lakes where management actions are applied (Jeppesen et al. 2005). In the case of endemic ancient lake species, source populations may not be available to permit these species to rebound, even if water quality improves.

Human population growth

The contributing basins of the 29 lakes in our set contain a total human population of 256 million (3.5% of the world's population). Population density varies greatly across these lands, and some areas appear completely uninhabited (Pingualuit Lake in the Canadian subarctic) or very sparsely populated (Manicouagan Reservoir in the Canadian Subarctic, Lake El'gygytgyn in the Northeastern Siberian Arctic, and Lake Eyre in central Australia) (Fig. 5a). Nine of the lakes contain one or more large urban centers (> 300,000 people) within the catchment, led by the Caspian Sea (43 large urban centers), Aral Sea (six urban centers), and Lake Maracaibo (five urban centers). These are followed by Lakes Tanganyika (four large urban centers), Victoria (4) Baikal (2), Valencia (2), Malawi (1), and Van (1) (UN DESA 2014). The lake with the greatest population density in the catchment, by far, is Lake Valencia, Venezuela (> 800 humans per km^2), where the adjacent cities of Maracay and Valencia contain ~ 2 million residents. The close proximity of these two cities has been linked to high-nutrient loading to Lake Valencia in the past (Jaffé et al. 1993), resulting in eutrophication and algal blooms (Fig. 6). Other populous catchments include

Lake Biwa in Japan (450 humans per km^2), Lake Bosumtwi in Ghana (440 humans per km^2), and Lake Kinneret in Israel (370 humans per km^2). Population can also vary substantially between seasons in lakes with heavy tourism, such as Lakes Ohrid and Tahoe.

Anthropogenic contributions of nutrients and other pollutants, through sewage and runoff, vary with factors such as watershed hydrology, wastewater treatment efficiency, and the distance of urban centers from lake shores. Such water quality degradation has been revealed through paleolimnological techniques (e.g., Lake Malawi, Otu et al. 2011), as well as long-term monitoring (e.g., Lake Tahoe—Jassby et al. 1995, Lake Ohrid—Matzinger et al. 2007). While signs of anthropogenic eutrophication have been reported in most of the ancient lakes (Supporting Information Table S4), information for many lakes is incomplete. Based on human population within the catchment and standard human N and P daily excretions (*see* Supplemental Information section), the highest potential human nutrient loadings occur in large lake catchments in central Asia (Caspian and Aral Sea; 474 Gg N/yr and 237 Gg N/yr; 59 Gg P/yr and 30 Gg P/yr, respectively) and Africa (Malawi, Tanganyika, Victoria; 47–204 Gg N and 6–25Gg P/yr). Nutrient budgets for Lake Victoria confirm major anthropogenic sources of nitrogen to the lake, possibly related to long-term depletion of soil nitrogen stocks, but also 84% of the anthropogenic nitrogen in the catchment does not reach the lake, possibly due to denitrification or limited fluvial transport in this dry climate (Zhou et al. 2014). Nutrient delivery to the Caspian and Aral Sea is extensively modified through hydrological alterations, including damming and diversion to support irrigated agriculture (Dumont 1998; Micklin 2007).
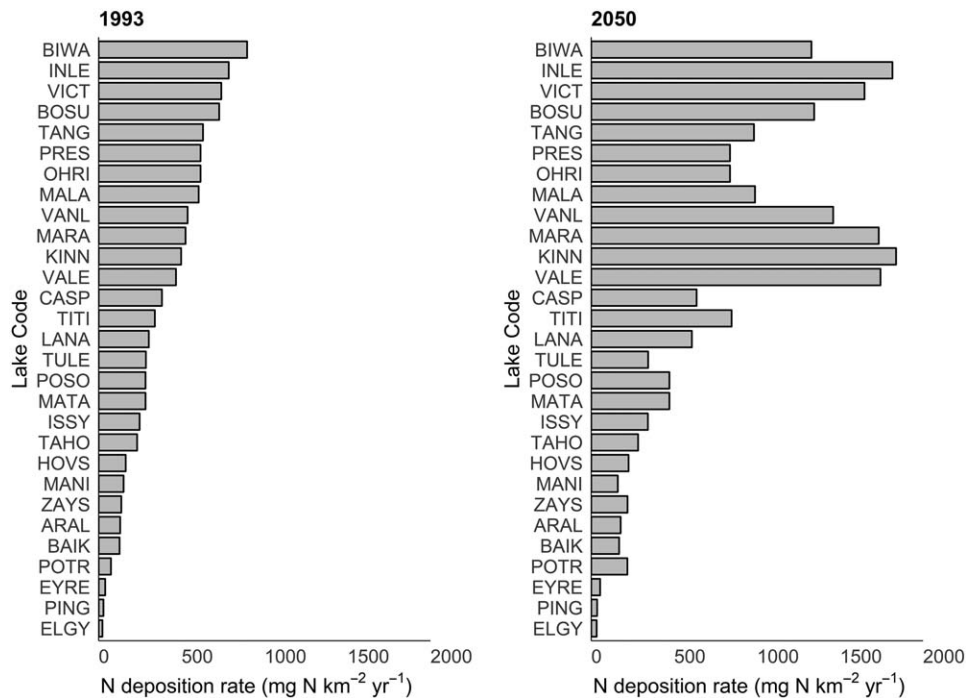
Fig. 7. N deposition to grid cells that contain the lakes. Estimates are from 1993 and projections are for the year 2050 (Dentener 2006).

Even relatively small human settlements on shorelines can contribute nutrients that fuel nearshore biotic growth and change, as has been demonstrated in Lakes Tanganyika (Kelly et al. 2017) and Baikal (Timoshkin et al. 2018). Localized effects of sewage can be dramatic; in remote Baikal, areas adjacent to small villages with rudimentary sewage management (Timoshkin et al. 2018) can shift from endemic periphyton to cosmopolitan filamentous green algae (e.g., *Spirogyra, Ulothrix*, and *Stigeoclonium*), while biological "black spots" exist near major sources of pollution in Ohrid (Kostoski et al. 2010).

Future growth in human population could increase loading of nutrients and other pollutants to many ancient lakes. Increases in human population densities between 1990 and 2015 have been most pronounced in the Lake Valencia catchment (increases of 14 people km^2 yr^{-1}), followed by Lake Bosumtwi (9 people km^2 yr^{-1}) and Lake Kinneret (7 people km^2 yr^{-1}) (Fig. 5b). There has been comparatively little population change in remote lakes of the Arctic and central Australia, and population declines have occurred around Lake Prespa and Lake El'gygytgyn, possibly associated with the fall of communism and associated migration.

Atmospheric deposition of nutrients

Along with sewage and runoff within watersheds, atmospheric deposition can be an important source of nitrogen and phosphorus to ancient lakes (Supporting Information Table S4). Several of the lakes discussed here occur in areas that were high-nitrogen deposition zones in 1993, the most recent available global estimates (Fig. 7), including East

Asia (Biwa, Inle > 780 mg N km^{-2} yr^{-1}), Africa (Victoria, Bosumtwi, Tanganyika, Malawi > 600 mg N km^{-2} yr^{-1}), central Eurasia (Prespa, Ohrid, Van > 500 mg N km^{-2} yr^{-1}) and South America (Maracaibo > 500 mg N km^{-2} yr^{-1}). Nitrogen sources are largely derived from fossil fuel power production, vehicle emissions, and agricultural activity (Vet et al. 2014). In general, N deposition to several ancient lakes in our set has increased with industrialization since the year 1860 (Supporting Information Table S1). The East African Rift Valley lakes (Tanganyika, Victoria, Malawi) are known for their high sensitivity to atmospheric deposition, because of their large surface areas and slow flushing rates (Hecky et al. 2006) with an estimated 55% P (Tamatamah et al. 2005) and 14% N deriving from atmospheric sources in Lake Victoria (Zhou et al. 2014). In Lake Maracaibo, wet atmospheric deposition accounts for ∼ 24% of total N loading (Morales et al. 2001). By the year 2050, it is projected that eight ancient lakes from our set will receive inorganic nitrogen deposition loads in excess of 1000 mg N km^{-2} yr^{-1}, including Lakes Victoria, Van, Bosumtwi, and Biwa, with the highest loads (> 1700 mg N km^{-2} yr^{-1}) in Lakes Kinneret, Inle, Valencia, and Maracaibo (Fig. 7).

Lakes with small catchment areas and large surface areas often receive a substantial share of their nutrient inputs directly from atmospheric sources (Broberg and Persson 1984; Shaw et al. 1989; Elser et al. 2009). For the 29 ancient lakes, catchment-to-surface area ratios (Fig. 3a) ranged from very low in crater lakes such as Pingualuit and Bosumtwi (∼ 1), to > 50 in lakes connected to major river systems, such

as Lake Eyre (125), Tule Lake (117), Aral Sea (69), and Inle Lake (59) (Fig. 3a). Slightly more than half of the ancient lakes had catchment-to-surface area ratios < 6. Several ancient lakes with relatively small catchment areas also have relatively high nitrogen deposition rates (Figs. 3c, 7), e.g., Lakes Bosumtwi, Victoria, Ohrid, Van, Maracaibo, Malawi, Biwa, Matano, Valencia, and Prespa. Nitrogen deposition at Lake Tahoe is implicated in 20th century increases in primary productivity and a switch toward phosphorus limitation (Jassby et al. 1995). For other lakes, the extent and effects of atmospheric deposition are not well studied.

Land use change

Urbanization and agricultural intensification are global phenomena occurring within the catchments of some ancient lakes (Fig. 5c). Crop cover ranged from 6% at Lake Biwa to around 80% at Lakes Kinneret and Victoria, and 97% in Lake Bosumtwi (ESA CCI 2014), although the latter has a very small catchment of 53 km^2, making the absolute area of agricultural land low. Despite the presence of major cities, the proportion of urban coverage within the catchments was generally low, except for Lake Valencia (21% coverage; Figs. 5, 6), Lake Biwa (7%), and Lake Ohrid (6%). Further analysis of land cover change between 2000 and 2010 showed that Lake Bosumtwi and Lake Matano had the highest rates of conversion to cropland (2% per 10 yr, Supporting Information Table S2). Several lakes in remote regions are surrounded by almost 100% natural vegetation cover. For example, Lakes Pingualuit, El'gygytgyn, Potro-k'Aike, and Eyre catchments had sparse vegetation cover due to Arctic or very dry conditions, while the watersheds of Lakes Manicouagan and Tahoe were predominantly forested.

While broader catchment land use change can be tracked via satellite imagery, more localized but sometimes extreme changes in aquaculture within lakes are more difficult to assess remotely. For example, in Lake Malawi, the arrival of tilapia aquaculture represented a significant new localized source of nearshore C, N, and P, which become diluted by currents mixing these pollutants to the larger body of the lake (Gondwe et al. 2011). In Myanmar, an expansion of Inle Lake's floating gardens contributes nutrients and pesticides to nearshore water (Akaishi et al. 2006) and has even been implicated in the decrease of open water area as vegetation takes over (Sidle et al. 2007).

Metals and emerging contaminants

In addition to nutrients, pollution by metals, plastics, and organic contaminants (e.g., EOC, PPCP, PhAC, etc.) are on the rise in several ancient lakes. Mining-associated metal pollution is well known in some of the ancient lakes (Supporting Information Table S4). Micro- and nanoplastics and emerging organic contaminants (EOCs) represent relatively new classes of pollutants with varied toxicity and effects, and highly varied concentrations across aquatic ecosystems

(Rosi-Marshall and Royer 2012 for EOCs; Lenart-Boroń and Boroń 2014 for metals; Driedger et al. 2015 for plastics).

Metals

Metals released from mining or industry can accumulate in aquatic systems (Salomons 1995; Foster and Charlesworth 1996; Dudka and Adriano 1997) and affect biota across multiple trophic levels (Boening 2000). Even after mine closure, drainage from remnant mine tailings and acid mining may continue to release metal pollution for many years (Dudka and Adriano 1997). Microbes, phytoplankton, invertebrates, and fish vary widely in their vulnerability to specific metals. Even sublethal concentrations can produce a variety of physiological, reproductive, and biochemical abnormalities in fish and other biota (Boening 2000; Clements et al. 2012).

Among ancient lakes, there is wide variation in mining and industrial activities along the shoreline and broader catchment. The associated metal pollution and management have drawn substantial attention (Supporting Information Table S4). Most early studies focus on detecting geochemical fate and transport of metals from mining, whereas more recent studies tend to incorporate biological responses to metal pollution. For example, elevated heavy metals have been reported in Lake Victoria (Onyari and Wandiga 1989; Kishe and Machiwa 2003; Machiwa 2010), although few of these studies have examined biotic responses. Metals typically associated with mining have also been noted in neighboring Lakes Malawi (e.g., Kidd et al. 1999; Kinnaird and Nex 2016) and Tanganyika (e.g., Benemariya et al. 1991; Chale 2002; Odigie et al. 2014) along with bioaccumulation in fish and waterfowl (Chale 2002). In Lake Tanganyika, uncertainty exists about the source of elevated Pb concentrations with some sediment records implicating watershed geology rather than mining (Odigie et al. 2014). Understanding these Pb accumulation patterns within Lake Tanganyika may present a unique opportunity to assess interplay between Pb and biotic community dynamics over centuries, which would not be possible in younger lakes. Multiple ancient lakes of Asia have been subject to metal pollution from mining, industry, and agriculture, including the Caspian Sea, Aral Sea, Issyk-Kul, Baikal, and Khovsgol (Fallah et al. 2011; Mashroofeh et al. 2012; Oughton et al. 2013). Much of this pollution is thought to be a legacy of mining in the former Soviet Union. For example, in the Caspian Sea, Al, Cu, Pb, Ni, Hg, and Zn were found to bioaccumulate in tissues of economically important fishes, rendering 60% of the catch unfit for purchase on the EU marketplace (Fallah et al. 2011; Hosseini et al. 2013). Sediment analyses at the mouth of the Haraz river, a major estuary flowing into the south Caspian Sea, indicated increased Cd, As, Sr, and Pb, indicative of heavy mining and industrial activity in the area, perhaps contributing to acidification (Nasrabadi et al. 2010). In the Aral Sea, elevated U originates from the Syr Darya River (Friedrich 2009), perhaps with intensified

ecological impacts following the dramatic declines in Aral Sea water volume. Similarly, in Lake Issyk-Kul, remnant mining from the 1950s and 1960s has been shown to transfer U and Ra through food webs, with bivalves, plankton, and vascular plants all showing increased ^{238}U and ^{226}Ra concentrations (Oughton et al. 2013). More recent mining activities are unfolding in Mongolia, within the vicinity of Lakes Baikal and Khovsgol, including Au and Cu/Mo mining. While heavy metal pollution from this mining activity has not yet been found in Lake Baikal, the mining sites have elevated Cu, Mo, and Zn concentrations up to 50 km away in the Selenga River (Brumbaugh et al. 2013), thus demonstrating the potential for metals transport in this changing region. Similarly, in Lake Titicaca Hg levels remain moderately low, despite extensive contamination from mining in adjoining regions (Guedron et al. 2017).

Plastics and microplastics

In aquatic environments, plastic fragments can harm wildlife by obstructing the gastrointestinal tract when ingested, restricting movement or growth by entanglement, and leaching harmful organic contaminants (e.g., PCBs) into the water (Derraik 2002; Teuten et al. 2009). While much of the attention on plastics and microplastics has been in marine systems (Zarfl and Matthies 2010; Van Cauwenberghe et al. 2013), freshwater, and terrestrial systems also receive these materials (Browne et al. 2007; Wagner et al. 2014).

In general, the status and influence of plastics in ancient lake ecosystems remains an open question for research. In Lake Victoria, microplastics have been found in the gastrointestinal tracts of both the Nile perch and Nile tilapia (Biginagwa et al. 2016), two economically important fish for the region. In Lake Khovsgol, Mongolia, Free et al. (2014) reported average concentrations of $>20,000$ plastic particles km^{-2} of lake surface area, four times the concentration found in Lake Superior, despite the relatively small population of 6000 people living in the catchment of Lake Khovsgol. These plastics include plastic fragments, films, and lines (Free et al. 2014), and likely originate from household plastic items, suggesting links to human activities on the lake or very near shore. To date, there are few other primary literature examples of plastics research in ancient lakes, though it is now an area of increasing interest in freshwater more generally (Horton et al. 2017).

Emerging organic contaminants

Effects of pesticides on aquatic systems have been studied since the 1970s, and recent research has included organochlorine and organophosphate compounds as exceptionally potent insecticides (DeLorenzo et al. 2002), but the biological responses to pharmaceuticals and personal care products (PPCPs) and their metabolites are less well known. PPCPs are produced by pharmaceutical and manufacturing industries (Pal et al. 2010) and can enter the environment via multiple pathways, including wastewater treatment systems (e.g., septic tanks and sewer systems) or industrial agricultural

practices (Heberer 2002). Because many EOCs are designed to be physiologically active at low concentrations, special concern has been placed on their ecotoxicological impacts throughout food webs (e.g., Lagesson et al. 2016; Meador et al. 2016), including algae (e.g., Lai et al. 2009; Rosi-Marshall et al. 2013), aquatic insects (e.g., Dietrich et al. 2010; Fong and Ford 2014; Lee et al. 2016), fish (e.g., Jobling et al. 2005; Olivares-Rubio et al. 2015), and amphibians (e.g., Tompsett et al. 2012). Long-term exposures to small concentrations (e.g., ng/L) can have adverse effects on growth and development of organisms, and ultimately on ecosystem function (e.g., Hoppe et al. 2012; Rosi-Marshall and Royer 2012; Fong and Ford 2014).

While there have been relatively few studies of EOCs in ancient lakes, many of these compounds are likely present due to the adjacent human settlements and activities such as recreation, fishing, agriculture, and aquaculture. In Lake Baikal, organochlorines associated with the cleaning of railway cars are the suspected cause of gastropod "cemeteries," which have been observed on the northern shore (Timoshkin et al. 2016). In Lake Victoria, residues of banned organochlorine and organophosphorus pesticides have been detected (Musa et al. 2011), along with elevated concentrations of estrogen compounds (Mdegela et al. 2014). Also in Victoria, Odada et al. (2004) suggested that improper disposal of expired pesticides, medical waste, petrol station wastes, and bunkering wastes were concerns around the lake, and along tributaries. Lake Biwa, Japan's largest lake, provides drinking water for millions of people yet receives notable point and nonpoint pollution, including sewage effluent containing substantial 17 beta-estradiol, a major form of the activated estrogen hormone and a common constituent in hormone supplements (Matsui et al. 2002). In the shallow southern basin of Lake Titicaca, which receives drainage from the city of La Paz, recent studies show high levels of antibiotics used in treatment of both human and animal disease (Duwig et al. 2014). Overall, very little is known about the extent to which EOCs alter ecosystem function and community structure in ancient lakes, as well as their absolute or general prevalence in the majority of ancient lakes.

Species introductions

Introduction of non-native species is one of the main threats to biological diversity in ecosystems worldwide (Sala et al. 2000; Doherty et al. 2016), including in many ancient lakes where dozens of non-native species have been introduced over the past decades (Supporting Information Table S4). The sources of invasive organisms to ancient lakes have included both intentional introductions (usually for augmentation of fisheries) and unintentional transport, either independently or along with intentionally introduced species. The magnitude and nature of the ecological impacts of species invasions in ancient lakes are diverse; in some cases,

impacts have been magnified through interactions with other anthropogenic influences such as eutrophication or overfishing (Balirwa et al. 2003; Alamanov and Mikkola 2011). Some introductions (e.g., Nile perch in Lake Victoria) had large ecological or social consequences (Hall and Mills 2000); the impacts of other invasions have been more muted while the effects of some are not yet fully understood or documented. Below, we highlight examples of intentional and unintentional introductions (also *see* Supporting Information Table S4).

The release of the Nile perch (*Lates niloticus*) and three tilapia species (*Oreochromis* spp.) into Lake Victoria may be the best documented and most ecologically and socially impactful intentional species introduction in an ancient lake. All four species were introduced into Lake Victoria in the 1950s and 1960s by the British colonial authorities in Uganda to improve the fishery of the lake, which previously relied on endemic haplochromine cichlids and tilapias (Hall and Mills 2000; Pringle 2005). Nile perch, a voracious piscivore, decimated the endemic fish community, leading to the disappearance of more than half of the lake's 500 endemic cichlid species and large alterations to community and food-web structure in the lake (Ogutu-Ohwayo 1990; Hall and Mills 2000). The negative impacts of Nile perch on the Lake Victoria ecosystem and its endemic species are thought to have been exacerbated by overfishing of the stocks of endemic species and the rapid eutrophication of the lake since the second half of the 20th century (Balirwa et al. 2003; Hecky et al. 2010). The ecological consequences of the introduction of Nile perch to Lake Victoria have been accompanied by large economic and social change. In the late 2000s, Nile perch dominated the economic value of the fishery on Lake Victoria (the world's largest freshwater fishery), supporting a \$350 million yr^{-1} export industry and millions of people in Uganda, Kenya, and Tanzania (Mkumbo and Marshall 2015). The refocusing of fishing effort toward Nile perch and the creation of a large export industry around the lake also had important social consequences, leading to a decline in small-scale subsistence fishing in favor of mechanized fishing fleets and the redistribution of people and capital (Riedmiller 1994; Hall and Mills 2000; Mkumbo and Marshall 2015).

Many other ancient lakes have experienced intentional introductions of fish in an effort to establish or augment local fisheries. Lake Biwa is now home to bluegill sunfish (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) which have been spread throughout Japan by anglers, and implicated in declines of endemic littoral fish species through predation and competition (Kawanabe 1996; Nishizawa et al. 2006; Sugiura and Taguchi 2012). Lake Sevan trout (*Salmo ischchan*), pike-perch (*Sander lucioperca*) and a number of other species were introduced to Lake Issyk-Kul by Soviet authorities in efforts to increase fishery yield (Alamanov and Mikkola 2011). These introductions, together with overfishing, led to declines in abundance and

near extirpation of endemic species (Alamanov and Mikkola 2011). Efforts at fishery improvement led to the introduction of Lake Trout (*Salvelinus namaycush*), Kokanee salmon (*Oncorhynchus nerka*), and Bonneville cisco (*Prosopium gemmifer*) into Lake Tahoe between 1888s and 1960s (Morgan et al. 1978; Vander Zanden et al. 2003). The zooplanktivorous opossum shrimp (*Mysis relicta*) was also intentionally introduced to Tahoe in the mid-1960s as a food source of Lake Trout. Rather than serving as prey for salmonids, mysids become their competitors, consuming the zooplankton on which juvenile fish depend and are widely blamed for the decline in salmonid production in Lake Tahoe (Spencer et al. 1991). Lake Kinneret in Israel has received several intentional and unintentional introductions of fish (Roll et al. 2007), as has Lake Titicaca (*see* "Fisheries and hunting" section). Lake Matano is home to at least 14 non-native fish species introduced both intentionally and unintentionally (Herder et al. 2012).

Besides fish, unintentional introductions of other invasive organisms into ancient lakes have also been common and may threaten their biodiversity or alter ecosystem functions. In the Caspian Sea, an invasive ctenophore, *Mnemiopsis leidyi*, has been associated with large changes to the lower food web and the collapse of economically important sprat fishery (Pourang et al. 2016). The invasive Asian clam (*Corbicula fluminea*) has made its way to Lake Tahoe where it is suspected of stimulating nuisance growth of benthic algae through nutrient excretion (Forrest et al. 2012). A number of invasive gastropods have recently been documented in Lakes Malawi, Tanganyika, Ohrid, Titicaca, and Kinneret; negative interactions between the invaders and native snails have been observed in some cases (Albrecht et al. 2009, 2014; Heller et al. 2014; Van Bocxlaer et al. 2015). Fish parasites and diseases have also been unintentionally introduced into ancient lakes, presumably transported along with stocked non-native fish. In Lake Ohrid, a nematode parasite first recorded in the 1970s seems to be linked to the artificial stocking of eel young (Cakić et al. 2002). In Lake Biwa, Uchii et al. (2013) associated mass die-offs of carp with the introduction of a cyprinid herpes virus into the lake.

Non-native aquatic plants have also been associated with environmental change in some ancient lakes. Water hyacinth (*Eichhornia crassipe*), a floating aquatic macrophyte native to South America, was accidentally introduced into Lake Victoria in the late 1980s and rapidly colonized the nearshore zone and bays of the lake, covering thousands of acres by the mid-1990s (Albright et al. 2004). The high densities of water hyacinth have been linked to severe economic losses related to disruption of fishing and transportation (Albright et al. 2004) and ecological change, including changes to fish diets, macroinvertebrate communities, and oxygen concentrations (Villamagna and Murphy 2010). The submerged aquatic plants, *Elodea canadensis* and *Egeria densa*, have become established in the nearshore of lakes Baikal and

Biwa (respectively) and have been linked to changes in habitat structure and water chemistry there (Hall and Mills 2000).

The number of species introductions and the extent of their ecological impacts vary among ancient lakes. Although some of these differences may be a function of uneven research effort directed toward different lakes, it is clear that the effects of species introductions have been severe in lakes such as Victoria, but less severe in lakes such as Baikal, Hovsgol, and Tanganyika (Hall and Mills 2000). Why some lakes have been less impacted by invasive species is unresolved and probably a complex function of the natural environmental context (such as temperature, productivity, and native community structure) and the identity and frequency of non-native species arrivals. Environmental change, including climate warming, eutrophication, and overfishing of native stocks may allow invasive species to increase in abundance (Hellmann et al. 2008; Rahel and Olden 2008) or entice fisheries managers to attempt new introductions. Continuing research, monitoring, and public education are necessary to better understand and control the threats of species invasions into ancient lakes.

Fisheries and hunting

Several ancient lakes have major fisheries that supply food for local populations and provide regional economic support. As persistent features of landscapes throughout the development of human civilization, ancient lakes have attracted human settlements that have often persisted through subsistence fishing (Vaillant et al. 2011; Capriles et al. 2014). Modern advances in fishing techniques and economic pressures have increased potential for overfishing and fishery collapse. Frequently, these pressures have been synergistic with efforts to augment fisheries with non-native species, resulting in unanticipated consequences such as the extirpation of native Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) in Lake Tahoe (Vander Zanden et al. 2003). Data on fisheries for ancient lakes tend to be localized, and not widely reported (Supporting Information Table S4); thus, we highlight only a few illustrative examples below.

The East African ancient lakes of Malawi, Victoria, and Tanganyika comprise the largest lentic freshwater fishery in the world (FAO 2016). Fish caught from the East African ancient lakes are a key protein source for tens of millions of East Africans, while fishing activities directly support the livelihoods of thousands more people through revenue acquired by fishing, trading, and attracting tourism (Bootsma and Hecky 1993). This multi-lake fishery contributes substantially to poverty reduction and food security in the bordering countries of Kenya, Uganda, Tanzania, Burundi, The Democratic Republic of Congo, Zambia, Malawi, and Mozambique.

Fisheries in Lakes Malawi, Tanganyika, and Victoria are relatively well-documented compared to many other African lakes. Approximate trends can be assessed using catch data from the major fish landing sites in each lake. These data suggest that fish catches in the early 20th century were low due to small numbers of fishers, fishing vessels, fishing gears, and fish markets (Verschuren et al. 2002). Large-scale commercial fishing became more widespread in the 1970s–1990s, sometimes coinciding with large increases in total catches, though robust data on long-term change remain uncertain due to the potential for underreporting (Watson and Pauly 2001). In some locations, large-scale commercial fishing has persisted, but many commercial fishing operations have declined or collapsed locally (Coulter 1970; Turner 1977; McCracken 1987; Hecky et al. 2010). The number of fishers and boats has increased rapidly, leading to sharp declines in the catch per unit effort (Ogutu-Ohwayo 1990; Ogutu-Ohwayo and Balirwa 2006; Sarvala et al. 2006).

The threats to fisheries in the East African ancient lakes of Malawi, Victoria, and Tanganyika are somewhat similar to those faced by many other ancient lakes of the world. Fishery unsustainability has been partially attributed to climate change (O'Reilly et al. 2003; Hecky et al. 2010; Tierney et al. 2010), species introductions (Achieng 1990; Genner et al. 2013), eutrophication (Hecky et al. 2010), pollution (Cohen et al. 1993; Coulter and Mubamba 1993), excessive fishing effort (Kaufman 1992), destructive fishing methods (Ogutu-Ohwayo and Balirwa 2006), capture of immature fish (Craig 1992), and weak fisheries management (Balirwa et al. 2003). As these stressors threaten the lakes' fisheries concurrently, they will often interact (Jackson et al. 2016) making it difficult to tease apart their relative effects, although the introduction of the Nile perch (*L. niloticus*) has been highlighted as a strong agent of change in Lake Victoria as described above in "Species introductions" section. Potentially interacting threats to the fisheries of the East African Rift Lakes include in situ cage aquaculture (Kassam et al. 2003), mercury pollution (Sindayigaya et al. 1994; Campbell et al. 2003; Kidd et al. 2003), and continued climate change (Tierney et al. 2010). Furthermore, differences in size, depth, and residence time among Lakes Tanganyika, Malawi, and Victoria could mediate the susceptibility to specific anthropogenic forcings (Kraemer et al. 2015). Thus, management efforts often attempt to contextualize the threats faced by the individual East African ancient lakes for more effective conservation, which also requires cooperation among neighboring countries and technological and financial contributions from the international scientific community at large.

Siberia's Lake Baikal has long been an important source of food to humans, and archeological evidence shows that fish and nerpa (endemic freshwater seal, *Pusa sibirica*) were exploited by indigenous people living around Lake Baikal since at least the mid-Holocene (Nomokonova et al. 2010). Early Russian settlers to the region heavily relied on fishing and seal hunting, and a commercial fishery was well-established in the region by the 18th century (Egorov and
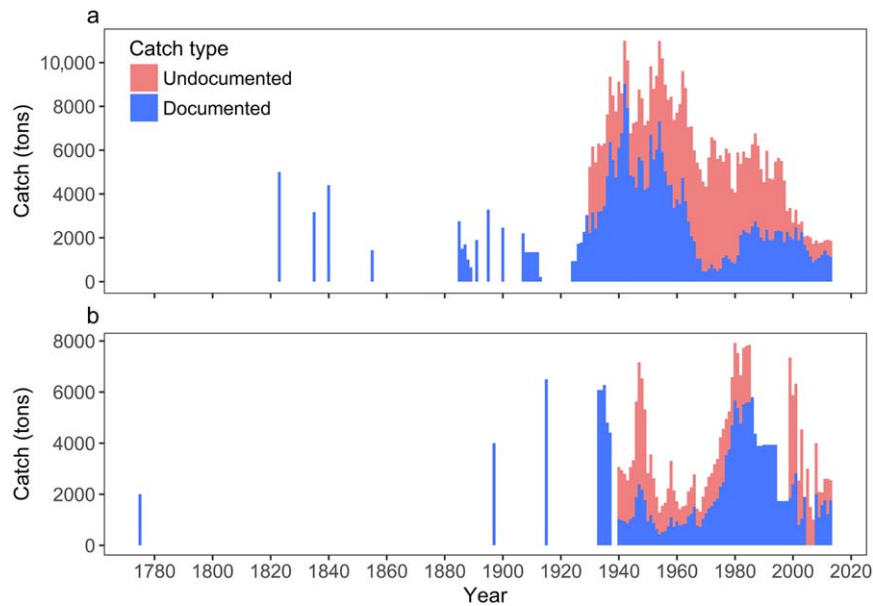
Fig. 8. Catch estimates for omul (**a**) and nerpa (**b**) in Lake Baikal, showing documented and estimated undocumented (illegal) catch. Catch values were obtained from the Russian literature (Egorov and Klimenchenko 1971; Pastukhov 1993; Mamontov 2009; Petrov 2009; MNRERF 2014). Where a range of values was given, the midpoint of the range was used.

Klimenchenko 1971). Although a wide range of species were targeted by indigenous and Russian fishermen, most of the commercial harvest effort has been focused on two endemic species: Baikal omul (*Coregonus migratorius*) and nerpa (Egorov and Klimenchenko 1971; Petrov 2009).

Harvest estimates and description of harvest methods for omul and nerpa go back to the early 19th and late 18th centuries, respectively (Fig. 8). In its early years, the commercial omul fishery was focused almost exclusively on fall spawning runs of omul into river mouths. The unsustainability of this fishing method was recognized as early as the 1820s, but it continued in some form until the 1950s, even after the establishment of a pelagic fishing fleet (Egorov and Klimenchenko 1971). Omul harvests fluctuated widely during the 20th century (Fig. 8a). Mechanization of the fishing fleet in the 1930s and high demand during the Second World War drove a rapid increase in harvests, which peaked at 10,000 tons/yr in the 1940s and 1950s. High-fishing pressure and unsustainable practices led to decreasing catches in the 1960s and severe fishing restrictions throughout the 1970s (Mamontov 2009). Today, the commercial harvest has stabilized at around 1000 tons/yr, below the official quota of 1500 tons/yr set by Russian regulators (Mamontov 2009; MNRERF 2014). The harvest of nerpa (mainly for the fur industry) has varied substantially throughout its recorded history (Fig. 8b). In the 20th century, harvests decreased during the Second World War and then increased to a peak of ∼ 6000 animals/yr in the 1980s. Commercial hunting has been prohibited since 2007, with harvest of 1500 animals/yr allowed only for indigenous people and for scientific

purposes (MNRERF 2014). Modern nerpa population size is estimated to be between 80,000 and 120,000 individuals (Petrov 2009; MNRERF 2014).

Management of the omul and nerpa harvest, however, is complicated by illegal harvesting (Mamontov 2009; Petrov 2009; MNRERF 2014). Poaching is difficult to quantify, but estimates suggest that harvests of omul by poachers have been consistently significant, reaching their peak during the period of severe fishing restrictions in the 1960s and 1970s. It is believed that poachers currently harvest slightly less than half of the "official" catch (Fig. 8a; Mamontov 2009; MNRERF 2014). Similarly, estimated illegal harvests of nerpa have fluctuated widely over past decades but remain pervasive (Fig. 8b, Petrov 2009).

Lake Titicaca: Co-occurring recent ecological changes

The anthropogenic impacts discussed above generally will co-occur in a single lake and catchment. Transboundary Lake Titicaca provides an example of the range of issues affecting ancient lakes. Lake Titicaca is a large ancient lake (area = ∼ 8562 km^2) located in the tropical Andes (Dejoux and Iltis 1992). Bolivia and Peru share the lake's catchment, and both countries rely on the lake for ecosystem services (e.g., irrigation, fisheries; Priscoll and Wolf 2010). Its altitude (3809 m above sea level) and latitude (16°S) result in high rates of solar radiation and evaporation that are coupled with large interannual variation in precipitation, driving fluctuating lake levels. Lake Titicaca is fed by several large rivers and many smaller streams, with major contributions from Rio Ramis and Rio Coata, and it has minor discharge

through a singular outlet, the Rio Desaguadero. The lake has two sub-basins (Lago Grande and Lago Huiñaimarca). Lago Huiñaimarca, Puno Bay, and several other bays are much shallower than the average depth of Lago Grande ($\sim$ 135 m) and are, therefore, much more vulnerable to eutrophication and pollution. Changes underway in the Lake Titicaca catchment include increasing human population, expanding agriculture, water-level manipulation, and mining.

Cities located on major tributary rivers and expanding urban areas near bays are a significant source of solid waste, sewage, and other pollutants to Lake Titicaca (UN WWAP 2003). Sewage released into the lake causes eutrophication and the proliferation of pathogenic bacteria and parasites. Chlorophyll concentrations imaged by satellite of Puno Bay on the Peruvian side of Lake Titicaca documented eutrophication as a result of untreated sewage disposal from the city of Puno and regional agricultural practices (ESA 2013). Massive algal blooms and degraded water quality also occur in Lago Huiñaimarca, and in several shallow bays of the large basin of Lake Titicaca. Antibiotics are a recently recognized emerging contaminant in Lake Titicaca, stemming from the release of urban wastewater into the Lake Titicaca catchment (Duwig et al. 2014).

Agriculture and industry also contribute to the eutrophication and pollution of Lake Titicaca. Within the catchment, much of the suitable land for farming is located in close proximity to the lakeshore (UN WWAP 2003), resulting in fertilizer and pesticide runoff. Agricultural practices have recently expanded in the catchment, leading to reduction of native sedge (totora) and wetlands, which have undergone extensive land-use conversion to agriculture over the period of 2003 to 2010 (ESA 2013). Sewage and agriculture contribute to high-metal concentrations in water, along with mining and industry throughout the watershed (Gammons et al. 2006; Choque et al. 2013; Monroy et al. 2014, Guedron et al. 2017). High-Pb concentrations in the river inlets and bays and elevated levels of heavy metals in fish tissue illustrate the widespread metal pollution of Lake Titicaca (Monroy et al. 2014).

In addition, species introductions have negatively impacted communities native to the lake. The introduction of the rainbow trout (*Salmo gardnerii*) was part of a plan in the 1930s to expand commercial fisheries within Lake Titicaca, especially in areas of the lake relatively depauperate of fish (Laba 1979; Hall and Mills 2000). This introduction was followed by the infiltration of the lake by the pejerry (*Odontesthes bonariensis*), a fish native to Argentina, in the 1950s (Laba 1979). Introduced species supported commercial fisheries with international canneries until the late 1960s (Hall and Mills 2000), which has impacted populations of native endemic fishes. Competition, predation of fry, and the likely introduction of parasitic protozoa from fish stocking drove down populations of the native *Orestias* spp. (pupfish) and may be responsible for the extinction of endemic *Orestias*

cuvieri (Laba 1979; Wurstbaugh and Tapia 1988; Hall and Mills 2000). Lake Titicaca's exotic species are not limited to planned introductions; recently the globally invasive gastropod *Physa acuta* has been identified in Puno Bay, which may pose a threat to the endemic gastropod fauna in Lake Titicaca (Albrecht et al. 2009).

Future research opportunities in ancient lakes

At least three facets of ancient lakes invite greater attention worldwide—the ecology of their unique flora and fauna, their paleolimnological history, and their long association with human populations. High endemism has resulted from long histories of isolation, persistence, and speciation in the ancient lakes. Thus, while many of the threats to these ecosystems are shared with younger ecosystems, the unique heritage of ancient lakes may be impossible to restore with remedial human action. Accompanying this history of evolution among biota has been a long-term accumulation of information about regional and global paleohistory, stratum by stratum, in the sediments of ancient lakes (Wilke et al. 2016). Together with human histories compiled by archaeologists, such ecological information could be used to piece together not only the relationship of lakes with climate, but also the relationship of lake resources with surrounding people (Capriles et al. 2014).

Anthropogenic effects on biodiversity

What are the ecological circumstances under which speciation occurred, and might these past conditions provide clues to anticipate changes in ecosystem processes in lakes where endemic biota play significant roles? In ancient lakes with a history of extensive speciation at extremes of temperature, or precipitation, anticipating biological changes in response to warming is difficult but potentially important; e.g., Lake Baikal endemics tend to be coldwater stenotherms with optimal growth at low temperatures (e.g., Kozhov 1963; Kozhova and Izmest'eva 1998; Bondarenko et al. 2006; Katz et al. 2015; Izmest'eva et al. 2016; Bedulina et al. 2017) and behavioral avoidance of warm water (Timofeyev and Shatilina 2007; Axenov-Gribanov et al. 2016; Jakob et al. 2016), while endemic cichlids of the African Rift Lakes are adapted to high temperature but already may be living near physiological maxima. Climate is not the only significant contributor to changes in selective pressures that might affect biodiversity. Evolution of the biota of African ancient lakes appears to have occurred under conditions of low turbidity, in which visual cues helped to reinforce species boundaries via changes in mating and reproduction, such that eutrophication or other reductions to water clarity may drive genetic change (Seehausen et al. 1997). Eutrophication is also thought to threaten endemic species at Lake Ohrid where, together with warming temperatures (Matzinger et al. 2006), it may lead to episodic or long-term anoxia of the bottom layer that stresses a uniquely endemic gastropod community

(Stanković 1960, Albrecht and Wilke 2008). Similarly, in Lake Titicaca, macroinvertebrate community structure and diversity and the viability of endemic macrophytes are inversely correlated with distance from urban areas and associated wastewater discharge, which affect changes in water-column oxygenation and the associated microbial communities (Costantini et al. 2004). Such topics may provide a productive ground for interaction between ecologists and the evolutionary biologists who have produced an impressive literature on speciation in ancient lakes (e.g., reviewed in Martens 1997; Schön and Martens 2004, Cristescu et al. 2010).

Paleolimnology: Long-term ecology and biodiversity

Lake sediment records provide unparalleled opportunities to deepen our understanding of the resilience of these ancient ecosystems to anthropogenic disturbance, and provide insights into the ecological dynamics that bridge timescales occupied by community ecologies and deep-time phylogeny (Seddon et al. 2014; Jackson and Blois 2015). In particular, understanding the resilience of lake communities to anthropogenic drivers and the processes underlying species extinctions is important if we are to manage lake ecosystems for the future benefits of humankind. Paleolimnology uniquely allows the definition of "natural" envelopes of community variability, to identify tipping points and species extirpations or extinctions (Randsalu-Wendrup et al. 2016). Safe operating spaces in the form of planetary boundaries have recently been refined for blue water use, and also for biogeochemical flows related to nitrogen and phosphorus impact on lakes (Steffen et al. 2015). For example, it is clear that sustainable environmental water flows for the Aral Sea and its watershed have been greatly exceeded since the 1960s. However, using palaeolimnology, Austin et al. (2007) exploited the sensitivity of diatoms in the Aral Sea to changing water chemistry as declining lake levels led to increased concentrations of solutes. Quantitative reconstructions showed that environmental water flow had also been substantially disrupted during the 13th and 14th centuries due to a combination of human impact and climate change. These recurring dramatic changes of the Aral Sea could be responsible for the low levels of endemism in the lake, e.g., mollusc remains in Aral sediments show only cosmopolitan species persisted in the lake for the past 1000 yr (Filippov and Riedel 2009). Elsewhere, Verschuren et al. (2002) used diatom and chironomid analyses of sediments in Lake Victoria to show that eutrophication has resulted in the loss of deep-water oxygen since the 1960s, which contributed to the extinction of some deep-water endemic cichlids, in addition to impacts linked to the introduction of the Nile perch. Geochemical indicators in lake sediments can also integrate pervasive ecological effects, such as when recent warming enhanced thermal stratification in Lake Tanganyika and reduced nutrient upwelling, thereby leading to a decline in lake productivity (O'Reilly et al. 2003). Long diatom records from ancient

lakes are also important in developing hypotheses on how cosmopolitan and endemic taxa will respond to environmental stressors (Spanbauer et al. 2018), which can be tested experimentally (Saros 2009).

Sedimentary ancient DNA (*seda*DNA) analysis is a recent technique that may greatly expand knowledge of past biodiversity in ancient lakes. However, despite its promise, to date the exploitation of *seda*DNA in lakes as a reconstruction technique has had mixed results. Bulk sediments contain a complex set of genetic material from many different types of organisms, as encountered in environmental DNA analyses (e.g., Anderson-Carpenter et al. 2011; Pansu et al. 2015). Recent technological developments, such as next generation sequencing, may create opportunities for *seda*DNA to provide complementary information to existing proxies, especially with regard to biodiversity (Boessenkool et al. 2014) and long-term ecosystem dynamics (e.g., Anderson-Carpenter et al. 2011; Pansu et al. 2015), although technical uncertainties remain (Parducci et al. 2017).

Conclusions

While not all anthropogenic threats are unique to the ancient lakes, their long history makes them uniquely valuable to science and society. These lakes not only record long histories of environmental variation and human resource use, but also harbor high rates of endemism and biodiversity. Many of the endemic biota in ancient lakes may be especially sensitive to threats, and may be less likely to recover following population collapses. Compared to other kinds of change experienced over their long histories, the recent patterns of biodiversity loss and other degradation are occurring on comparatively short-time scales. Thus, these environmental impacts may strike deeper chords for local and regional communities whose cultures are strongly linked to the existence of ancient lakes.

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Conflict of Interest

None declared.

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