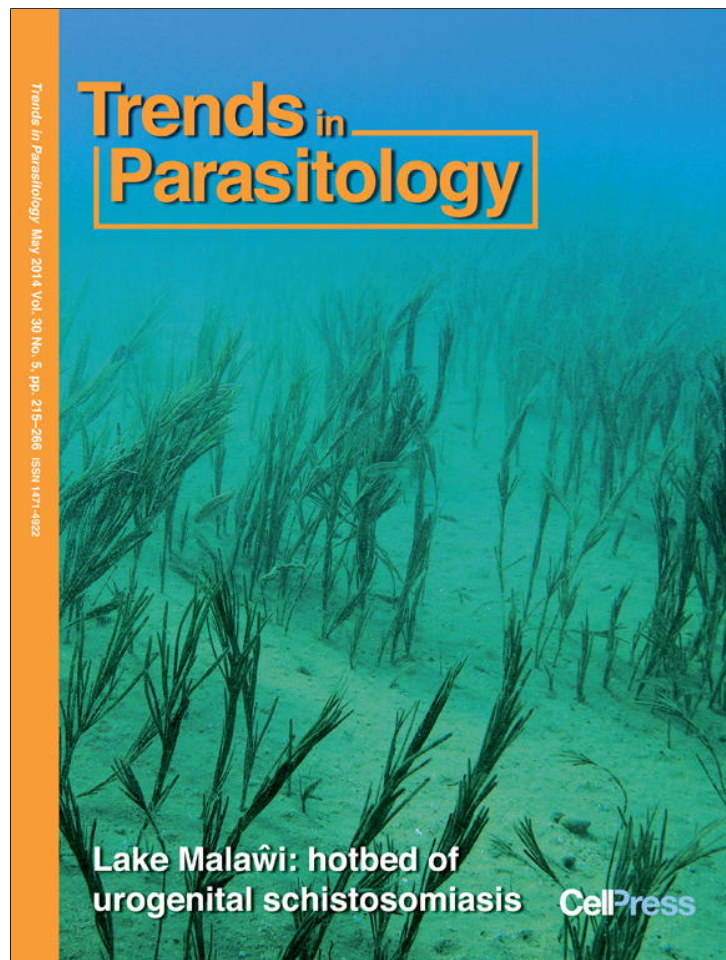


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Growing population and ecosystem change increase human schistosomiasis around Lake Malaŵi

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Multiple anthropogenic environmental stressors with reinforcing effects to the deterioration of ecosystem stability can obscure links between ecosystem change and the prevalence of infectious diseases. Incomplete understanding may lead to ineffective public health and disease control strategies, as appears to be the case with increased urogenital schistosomiasis in humans around Lake Malaŵi over recent decades. Sedimentation and eutrophication help explain historical changes in intermediate host range and parasite transmission. Hence, control strategies should account for abiotic changes.

Introduction

Human population densities are increasing in most parts of the world, and anthropogenic disturbances affect all ecosystems on the planet. Growing evidence indicates that these changes affect global health [1]. Multiple anthropogenic stressors regularly interact, which often hastens the deterioration of ecosystem stability beyond the anticipated effects from individual stressors alone [2]. Infectious diseases strongly depend on human–environment interactions for their transmission, and large-scale responses to climate and ecosystem change can be expected [1]. The existence of multiple, reinforcing, environmental stressors, however, creates the difficulty that aspects of ecosystem change and links of cause and effect may become elusive ([1] and references therein). Incomplete understanding of interaction mechanisms by scientists and/or policy makers can result in ineffective public health and disease control strategies. An important human health concern for which such mechanisms are vitally important is that of the increasing prevalence of human schistosomiasis around Lake Malaŵi over the past decades [3,4]. The link between increased human infection rates and the population densities of intermediate hosts has been documented extensively [4,5], but other interactions have not. Here, we address this issue and suggest that some neglected abiotic

factors favor parasite transmission and, hence, should be considered in control strategies.

Epidemiology

Schistosomiasis (bilharzia) is a tropical, debilitating parasitic disease that currently affects ~243 million people worldwide, with many more at risk, and causes major health problems, primarily in Africa [3,6] [World Health Organization (WHO) schistosomiasis fact sheet, <http://www.who.int/mediacentre/factsheets/fs115/en/index.html>; accessed January 2014]. The parasites, blood-dwelling flukes of the genus *Schistosoma*, have humans and pulmonate freshwater snails as definitive and intermediate hosts, respectively. An overview of transmission pathways and pathologies of human schistosomiasis is provided elsewhere [6]. Human infection occurs via parasite penetration through the skin during or directly after contact with waters inhabited by infected intermediate hosts [6]. In Malaŵi, urogenital schistosomiasis prevails, which is transmitted by the snail *Bulinus nyassanus* along sandy, open shorelines of Lake Malaŵi, and by *Bulinus globosus* in inland swamps, ponds, and possibly even bays of Lake Malaŵi rich in macrophytes and detritus [5] (Figure 1). In some villages surrounding Lake Malaŵi, ~73% of the people and ~94% of the schoolchildren are infected; the prevalence is lower inland, but still substantial and increasing (10–26% and 15–57%, respectively) [5].

Investigations of the increased prevalence of urogenital schistosomiasis around Lake Malaŵi [4,5,7] suggest that overfishing and the collapse of molluscivore fish stocks were strong drivers of the observed population expansions of the intermediate snail host, especially in shallow water (Figure 2), and, hence, increased transmission of the disease. Consequently, restoration of molluscivore fish densities presented a biological control mechanism. The correlation between abundance data of predatory fish and *Bulinus* snails is certainly striking, but this pattern may not be the sole or primary cause of increased human infections. Below, additional factors prominently affecting the functioning of freshwater ecosystems and possibly the transmission cycle of schistosomes are highlighted. We focus on the shores of Lake Malaŵi near Chembe (Cape Maclear), where the prevalence of schistosomiasis is highest and historically most monitored (Figure 1).

Schistosomiasis results from an interaction between parasite, intermediate host, and definitive host. The abundance of the parasite is strongly dependent on the reciprocal transmission between intermediate and definitive

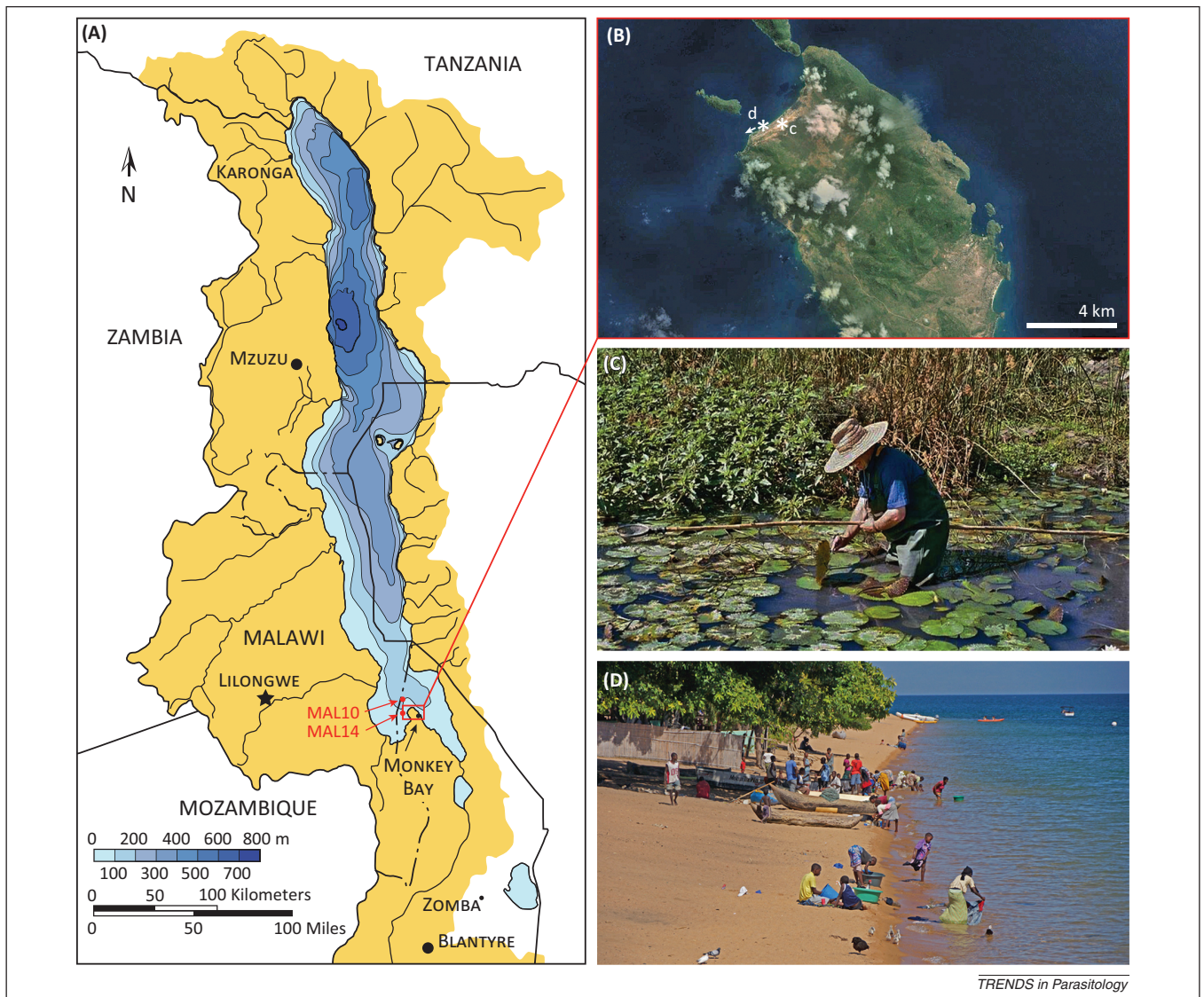
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TRENDS in Parasitology

Figure 1. Lake Malaŵi and transmission sites for urogenital schistosomiasis. The Malaŵi Basin (A) with its hydrographic catchment in yellow, lake bathymetry in shades of blue, and in red the position of the two cores (MAL10 and MAL14) for which data are provided in Figure 2D; (B) a satellite image of the Nankumba Peninsula (© Google Earth and DigitalGlobe; accessed February 2014 via Google Earth), with position and direction in which (C) and (D) were taken; (C) swamps nearby the Chembe river represent the habitat of *Bulinus globosus*; (D) the sandy shoreline at Chembe is a major within-lake transmission site for urogenital schistosomiasis with *Bulinus nyassanus* as intermediate host.

hosts. Without reciprocal transmission, the disease would not subsist, because intermediate hosts do not infect each other directly, and neither do definitive hosts [6]. Schistosome abundance is thus a function of the population densities of the intermediate and definitive hosts, and the likelihood of successful transmission upon interaction between them. To our knowledge, limited data exist on possible evolutionary trends in *Schistosoma* virulence (e.g., changes in host-finding behavior) and how immune resistance changes in humans after years of exposure [6]. Nevertheless, the production of human-infectious cercariae by the intermediate host increases dramatically with temperature [8], and because surface water temperatures of Lake Malaŵi are increasing [9] transmission may intensify. Several other environmental factors, for example, the frequency and intensity of rainfall during the rainy season, may also have a strong but poorly documented effect.

Interaction mechanisms

Human population densities have more than doubled in Malaŵi over the past 30 years and follow a quasi-exponential curve (Figure 2A) (World Population Prospects: The 2012 Revision, United Nations Department of Economic and Social Affairs, <http://esa.un.org/unpd/wpp/index.htm>; accessed December 2013). Population densities of the intermediate host in shallow waters of Lake Malaŵi increased even more over this period (Figure 2B). The observed increase in the abundance of definitive and intermediate hosts in Malaŵi requires the availability of sufficient resources. Since the 1980s, human land use has intensified to sustain population growth; the area of agricultural land increased 1.5-fold and crop yield increased 1.6-fold approximately [Food and Agriculture Organization of the United Nations (FAOSTAT), <http://faostat3.fao.org/faostat-gateway/go/to/download/Q/QC/E>;

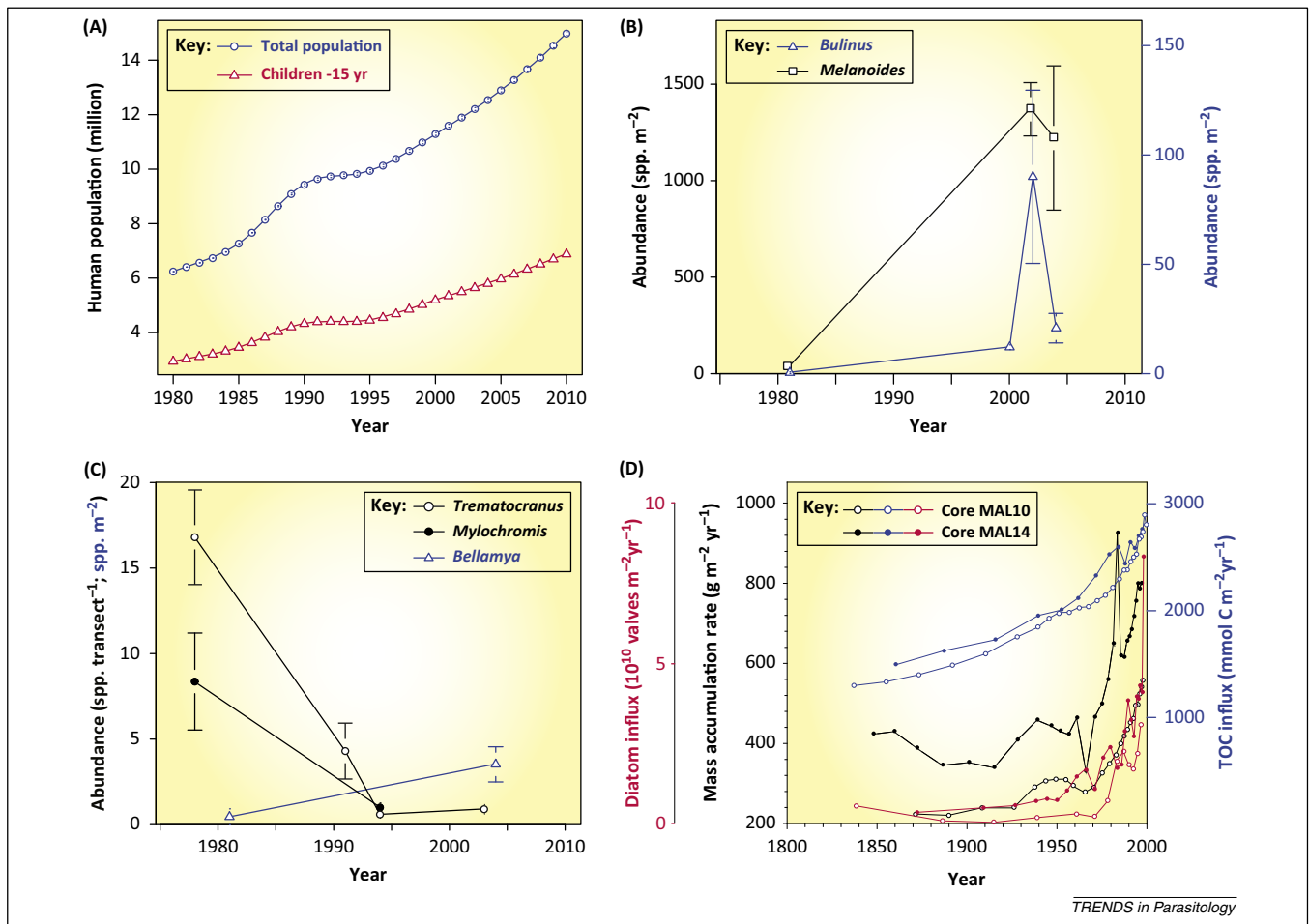


Figure 2. Host abundance and ecosystem change explaining increased schistosomiasis. Changes over the last decades in (A) the human population of Malaawi (total and children younger than 15 years; data from the United Nations Department of Economic and Social Affairs website, <http://esa.un.org/unpd/wpp/index.htm>; accessed January 2014) and (B–D) the benthic ecosystem of Lake Malaawi at Cape Maclear, a major schistosome transmission site. The abundance of (B) *Bulinus* and *Melanoides* increased drastically over the past decades, which relates to overfishing of (C) the main molluscivorous fishes *Trematocranus* and *Mylochromis*, but also *Bellamyia* gastropods, a prey not preferred by these fishes, increased markedly in abundance [4,5,11,13,15] and references therein). Abiotic changes in two sediment cores from the area put these observations in perspective: (D) the sediment influx (mass accumulation rates) increased markedly, which caused elevated influxes of total organic carbon (TOC) and diatom valves [10], providing therewith the nutrients that can sustain higher biomasses in the benthic ecosystem. Bars indicate 95% confidence intervals.

accessed January 2014]. Consequently, a gradual increase in sedimentation loads has been observed on littoral and sublittoral substrates in the south of Lake Malaawi, with associated increases in the influxes of total organic carbon (TOC) and microorganisms (diatoms; Figure 2D) to the benthic ecosystem [10]. Accelerated nutrient enrichment and soil erosion likewise changed phytoplankton communities [10], and sedimentation decreased benthic habitat heterogeneity [11]. The *Bulinus* species responsible for schistosome transmission in Lake Malaawi, and other gastropods such as *Melanoides*, are detritus feeders that inhabit sandy substrates [11,12]. Hence, increased sedimentation creates a more favorable habitat, and the higher organic content provides more nutrients for these taxa [11]. Intensified runoff and associated effects are known to have increased the carrying capacity in *Bulinus* species elsewhere [12]. Because sedimentation and the increased nutrient influx derive largely from changes in land use and runoff, the effects are unlikely to be limited to the lake itself, but probably also affect smaller ponds and swamps. Hence, inland *Bulinus* populations and associated schistosome transmission may likewise augment.

Based on environmental change and given the highly similar habitat and nutrient requirements of *Bulinus nyassanus* and co-inhabitants of the genus *Melanoides* [11,12], a positive spatial correlation in occurrence/abundance between both taxa in Lake Malaawi can be expected. Such a correlation is indeed observed [13] (B. Van Bocxlaer *et al.*, unpublished) despite the general tendency of freshwater pulmonates to have highly fluctuating population sizes (Figure 2B) [12], and it is difficult to explain solely with biotic interactions. First, *Melanoides* is used effectively elsewhere as a biological control agent for the snail hosts of schistosomes. Second, *Bulinus* is a preferred food for molluscivorous fish, even though *Melanoides* is dominant in these fishes' gut content (>70%) [14]. The abovementioned spatial correlation and the increase in population densities of gastropods that are not preferred food sources for predators (e.g., *Bellamyia* abundances increased approximately 7-fold from 1981 to 2003; Figure 2C) suggest that abiotic drivers such as increased sedimentation and eutrophication affected the intermediate hosts and other benthic taxa drastically.

Beyond overfishing, other important biotic stressors affect the benthic ecosystem, for instance, the mentioned changes in the phytoplankton community and biotic globalization. Examples of biological invasions that probably affect schistosome infections in humans around Lake Malawi are the hypothesized invasion of a new *Schistosoma* strain [7] and the arrival of an Asian morph of *Melanooides tuberculata* in the 1980s [13]. This *M. tuberculata* morph became dominant (currently ~75% of all *Melanooides* specimens in quantitative samples), has a more weakly ornamented shell than the native *Melanooides* morphs/species, and thus may be more prone to fish predation than these indigenous *Melanooides*. Current studies do not distinguish between native and invasive *Melanooides* morphs in trophic interactions, but it is possible that the preference by molluscivorous fish for *Bulinus* prey over the invasive *Melanooides* morph compared to the native *Melanooides* is diminished. If so, and given that *Melanooides* is dominant in both the environment and the gut content of predatory fishes, pulmonate consumption rates may be too low for molluscivorous fishes to act as a biological control mechanism, which was observed elsewhere.

Concluding remarks

Increasing human population densities, altered land use, and aquaculture efforts have strong effects on the ecosystems of the African Great Lakes, for example, by increased eutrophication and sedimentation ([9] and references therein). Lake Malawi and other water bodies in Malawi are undergoing drastic biotic and abiotic changes [4,5,9,10,13]. These changes and increasing human population densities appear highly favorable for schistosome transmission. Given that the effects are nonlinear, more holistic approaches that include monitoring of the abiotic setting of freshwater ecosystems and the study of feedback mechanisms are urgently needed. Restoring population densities of predatory fish would help biological conservation, stabilize trophic interactions in the lake, and contribute to controlling the transmission of schistosomiasis, but it needs to be combined with other strategies to optimize beneficial effects on human health. Terrestrial and freshwater ecosystems are strongly interlinked, and nutrition demands of the growing human population inspire more intensive ecosystem use. Combining an integrated control program for schistosomiasis, drug treatment, safe drinking water provisions, pit latrines, and continued biologic control of the intermediate snail hosts with efforts towards sustainable resource use are integral for optimal

improvement of human health. We also advise ameliorated community-based health education of the local population to enhance receptivity towards contributing to control strategies. Beyond the direct links of cause and effect, interaction mechanisms should be addressed. Additionally, more effective communication to tourists is recommendable given the increasing risk of infection.

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