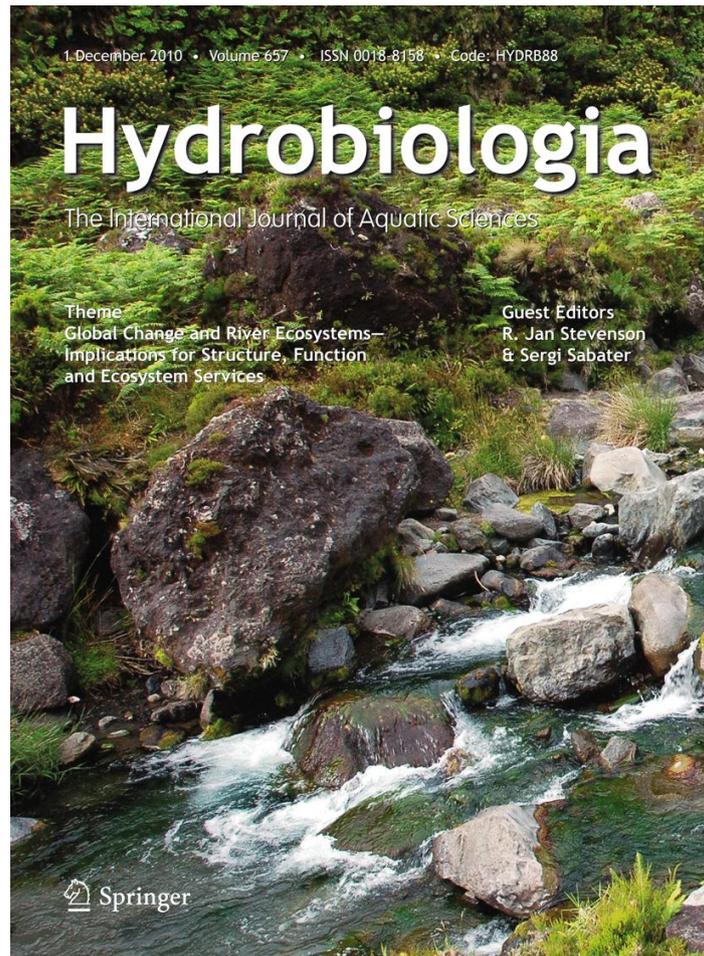


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Biogeochemical implications of climate change for tropical rivers and floodplains

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Abstract Large rivers of the tropics, many of which have extensive floodplains and deltas, are important in the delivery of nutrients and sediments to marine environments, in methane emission to the atmosphere and in providing ecosystem services associated with their high biological productivity. These ecosystem functions entail biogeochemical processes that will be influenced by climate change. Evidence for recent climate-driven changes in tropical rivers exists, but remains equivocal. Model projections suggest substantial future climate-driven changes, but they also underscore the complex interactions that control landscape water balances, river discharges and biogeochemical processes. The most important changes are likely to involve: (1) aquatic thermal regimes, with implications for thermal optima of plants and animals, rates of microbially mediated biogeochemical transformations, density stratification of water bodies and

dissolved oxygen depletion; (2) hydrological regimes of discharge and floodplain inundation, which determine the ecological structure and function of rivers and floodplains and the extent and seasonality of aquatic environments; and (3) freshwater–seawater gradients where rivers meet oceans, affecting the distribution of marine, brackish and freshwater environments and the biogeochemical processing as river water approaches the coastal zone. In all cases, climate change affects biogeochemical processes in concert with other drivers such as deforestation and other land use changes, dams and other hydrological alterations and water withdrawals. Furthermore, changes in riverine hydrology and biogeochemistry produce potential feedbacks to climate involving biogeochemical processes such as decomposition and methane emission. Future research should seek improved understanding of these changes, and long-term monitoring should be extended to shallow waters of wetlands and floodplains in addition to the larger lakes and rivers that are most studied.

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Introduction

In the process of conveying water and materials from uplands to the oceans, large tropical rivers and their

floodplains are sites of intense biogeochemical activity associated with the passage of river water through highly productive floodplains and estuaries. Rivers and their floodplains provide important ecosystem services, supporting biodiversity, freshwater and marine fisheries, traditional human livelihoods and productive agricultural land (Junk, 1997). Many large tropical rivers have not been regulated by dams (Nilsson et al., 2005), and therefore retain seasonally variable hydrological regimes and periodically inundated floodplains, characteristics that exert important influence on aquatic biogeochemical processes and fluxes (Lewis et al., 2000). Extensive seasonal inundation in many tropical floodplains makes them major natural sources of methane emission to the atmosphere (Melack et al., 2004; Denman et al., 2007). Large tropical rivers are important in the delivery of nutrients and sediments to marine environments, and this material influx supports productive estuarine and coastal marine ecosystems (Cotrim da Cunha et al., 2008). Where rivers meet the oceans, deltas and estuaries are important sites of biogeochemical transformations including biological production, sediment retention and nutrient transformation (Bianchi, 2007).

This article reviews literature on whether climate-driven changes are already taking place in tropical ecosystems, how future climate change is expected to affect large tropical rivers and their floodplains, and the potential biogeochemical implications of these effects. Large tropical river systems drain catchments ranging from rainforest to dryland and from relatively pristine to heavily impacted by human activity. In all cases, climate change will affect biogeochemical processes in concert with other anthropogenic drivers, such as land use change, construction of dams and other river channel alterations and water withdrawals. Also, changes in catchment vegetation and land use likely will produce potential hydrological feedbacks to climate that remain poorly understood. Evidence reviewed here indicates that climate change potentially is expected to profoundly influence the biogeochemical processes that underpin ecosystem functions of large rivers and their floodplains and estuaries, most prominently via hydrological changes in the catchments and rising sea levels at the river mouths, but potentially also via a host of other interactions. Tropical river catchments encompass a broad range of climatic settings, human activity and geomorphology, and thus the

hydrological and biogeochemical implications of climate change will be variable across river systems.

Tropical river hydrology and climatic regimes

Major tropical river systems and their associated floodplains are described by Welcomme (1985) and include systems with largely natural hydrological regimes, such as the Amazon and Orinoco rivers of South America, as well as systems that have been strongly impacted by hydrological modifications including large dams, such as the Paraná River in South America and the Niger River in Africa. All of these river systems are seasonally variable in discharge and many have extensive floodplains and deltas, although large dams can reduce variability in discharge and inundation. Floodplains fringing large rivers typically include areas flooded by riverine overflow as well as areas subject to inundation from local sources that drains through floodplains into a river system (Mertes, 2000; Hamilton, 2008a). Large tropical rivers deliver ~35% of global freshwater discharge to the oceans (Vörösmarty et al., 1997).

Seasonal variation in temperature, precipitation and river discharge occurs over most of the tropics, and is most marked in the 'wet-dry tropics' (tropical latitudes higher than $\sim 10^\circ$), where climatic seasonality is driven by the shifting latitudinal location of the equatorial trough and the inter-tropical convergence zone (Talling & Lemoalle, 1998). Seasonal variation in temperature and river discharge may or may not be coincident in timing. For example, inundation of much of the Pantanal wetland of Brazil takes place in the warmer months (Hamilton et al., 1996), whereas river flooding in the Okavango Delta in Botswana coincides with the cool season (Ramberg et al., 2006). The Amazon River system drains catchments on both sides of the equator with roughly opposite seasonal discharge patterns and as a result the seasonality of discharge and floodplain inundation along the main stem is somewhat attenuated (Hamilton et al., 2002).

The El Niño-Southern Oscillation (ENSO) cycle, which is associated with sea surface temperature anomalies in the tropical Pacific, exerts considerable influence on precipitation patterns in the tropics and subtropics (Foley et al., 2002; Bates et al., 2008). ENSO variability partly explains the interannual

variability in river discharges and floods and droughts in regions as distant as southern Africa and Australia. Large tropical rivers with discharges that are particularly influenced by ENSO events include the Nile, Amazon, Congo, Paraná and Ganges (Khan et al., 2006). The erratic behaviour of tropical cyclones also contributes to the interannual variability in the hydrological regimes of tropical rivers in regions where much of the rainfall is associated with cyclonic activity, such as southeast Asia and northern Australia.

Floodplain waters are amongst the warmest surface waters in tropical regions because they tend to be shallow (and thus they concentrate heat accumulation and track short-term fluctuations in air temperatures) and they lie at low elevations. Water depths can be >10 m in the main channels of the largest rivers, but the mean depth on fringing floodplains is typically much less, and often not deep enough to develop persistent hypolimnetic anoxia, even in the permanent floodplain lakes (e.g. Hamilton & Lewis, 1990; Hamilton et al., 1990). Most discussions of thermal regimes in tropical fresh waters have dealt with large lakes, for which there are many published examples, and often these are deep enough to be seasonally stratified and many of the most studied tropical lakes lie well above sea level (Talling & Lemoalle, 1998).

Shallow and quiescent waters on floodplains or in rivers with little or no flow are more subject to diel temperature fluctuation in response to short-term gains and losses of heat. Diurnal stratification is characteristic of these waters, and is a phenomenon subject to change in a warming climate, as discussed later. An example of thermal seasonality in relatively shallow waters of tropical rivers and floodplains is presented in Fig. 1, which shows typical seasonal fluctuations in daytime temperatures in waters of the Brazilian Pantanal. Figure 2 shows a diel cycle of temperature during the late dry-season in a slowly flowing monsoon river of northern Australia.

Similar water temperatures, commonly exceeding 30°C, but not often approaching 40°C during the warm season, have been measured in other shallow tropical waters in the wet–dry tropics. For example, measurements made in a rice field pool of northeastern Thailand (~17.5°N latitude) by Heckman (1979) showed frequent maxima above 35°C. Water temperatures in more equatorial locations usually do not reach such extremes due to attenuation of solar radiation by clouds (Lewis, 1987). Also, floodplains

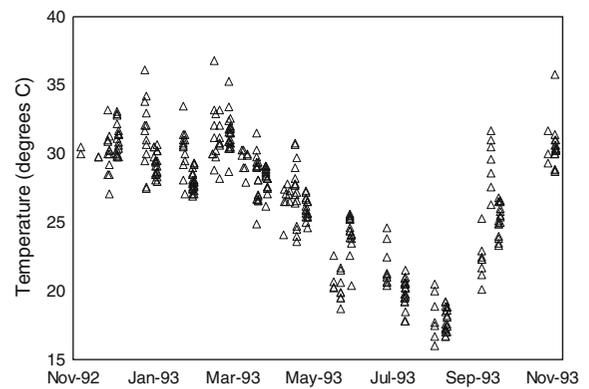


Fig. 1 Seasonal fluctuations in daytime temperatures in surface waters of the Brazilian Pantanal, collected by the author at numerous river and floodplain sites over the course of biogeochemical investigations (Hamilton et al., 1995). Most of the waters sampled were <3 m and many were <1 m deep, and were located between 17 and 18°S latitude

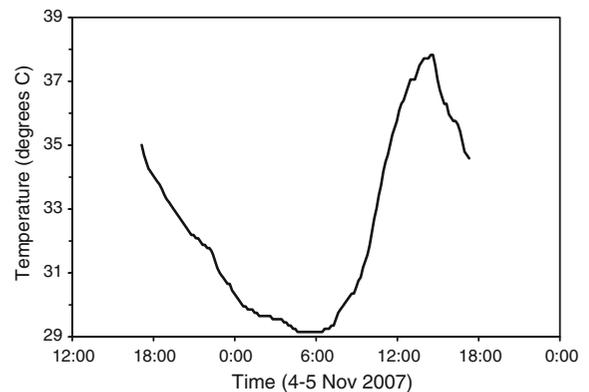


Fig. 2 Example of a diel temperature cycle in an open (uncanopied) riffle of a slowly flowing river of northern Australia during the late dry season (Mitchell River, 16.5°S latitude, 4–5 November 2007)

where precipitation is more equitably distributed throughout the year tend to have dense vegetation canopies that shade the water. Nonetheless, in shallow and uncanopied water bodies daytime water temperatures can surpass 30°C, as shown for example in data for an Amazon floodplain lake by de Melo & Huszar (2000), for Orinoco floodplain lakes by Hamilton et al. (1990), and in the Paraguay River by Hamilton et al. (1997). Thus, for this review, the water temperature range of interest is approximately 15–40°C, recognising that maximum temperatures above ~35°C are likely only in the shallowest waters.

Water temperatures in lakes and larger rivers are commonly measured although typically published only in summary form, obscuring the minima and maxima that can be important for biogeochemical and ecological processes. Temperatures in shallow waters of wetlands and floodplains are not measured as often, and when done so it is usually for a limited time, serving as ancillary information for studies focused on other topics. Long-term monitoring of water temperatures in a diversity of tropical water bodies, in conjunction with meteorological data collection nearby, would be a wise investment to improve our understanding of the thermal implications of climate change for aquatic ecosystems and could readily be done using inexpensive continuous logging systems, provided that rigorous calibration protocols were in place.

Climate change in the tropics: past trends and future projections

Current consensus on how climate change is projected to affect tropical regions is drawn mainly from the Intergovernmental Panel on Climate Change (IPCC) Technical Paper on Climate Change and Water (Bates et al., 2008), which is based on the Fourth Assessment Report (IPCC, 2007; Kundzewicz et al., 2008), and references cited therein. Additional information was drawn from CCSP (2008).

Temperatures in the tropics are projected to warm 2–4°C by 2100 (Meehl et al., 2007). The warming temperatures will extend tropical climates poleward and upward in elevation. Evaporation rates and atmospheric moisture fluxes are often projected to increase significantly as the temperatures rise because the saturation water vapour pressure increases non-linearly with temperature. However, evaporation rates are influenced by complex interacting factors associated with local geography and prevailing climatic conditions, and increases in atmospheric humidity and/or wind can counterbalance the temperature effect and even result in decreased evaporation rates (Hobbins et al., 2004, 2008).

Hydrological fluxes including precipitation, evaporation and runoff will intensify as a result of the increase in atmospheric temperature and moisture and consequent changes in atmospheric circulation. A general tendency in model projections for a warming

climate is that presently wet climates become wetter and dry climates become drier, and this appears to hold for the tropics as well as globally (IPCC, 2007). Increasing subtropical aridity is also projected, but mainly at the poleward flanks of the subtropics (Cook et al., 2008).

Timing and volume of river discharges respond strongly to changes in precipitation and are usually somewhat less sensitive to changes in evaporation rates and storage reservoirs (e.g. ground water, soil moisture, artificial reservoirs and in high-elevation catchments, snow and ice). Thus altered river hydrological regimes are expected to occur particularly as a result of changes in precipitation regimes. However, certain rivers also may change significantly in response to changes in evaporation rates, particularly in dryland catchments where a larger fraction of the precipitation is lost to evaporation (Goudie, 2006), as well as in high-elevation catchments such as the Himalayas where seasonal water storage as snow is important (Nijssen et al., 2001).

Many studies have searched for global trends in river discharge, precipitation and water quality over recent decades, but a clear consensus has yet to emerge. Recent study has pointed to an overall trend of increasing river discharge over the past century (Labat et al., 2004; Gerten et al., 2008), although the quality of the data set underpinning this conclusion has been questioned (Peel & McMahon, 2006; Milliman et al., 2008), and the increase has yet to be rigorously verified. Precipitation also fails to show discernable trends in total amount in the tropics (Bates et al., 2008), although trend detection is difficult in the face of high interannual variability in precipitation, in part, related to ENSO variation. While there may have been a global increase in river discharges, evidence so far indicates that trends across the tropics have certainly not been homogeneous (Bates et al., 2008), and are likely to be spatially variable in the future. For example, regional decreases in annual runoff have been noted for parts of West Africa and southern South America (Milly et al., 2005; Li et al., 2007). Recent assessments of trends in water quality also fail to show globally consistent changes that can be attributed to climate change (Bates et al., 2008). This lack of conclusive evidence for global trends is not surprising because hydrological changes associated with a changing global climate are expected to be spatially

heterogeneous and difficult to discern from natural variability and catchment-specific hydrological alterations by human activities.

Despite the ongoing debates about whether precipitation and river discharges have changed in the recent past, there is good reason to believe that a combination of global climate change and human interferences in land and river hydrology will increasingly alter river hydrological regimes in the future. Specific projections are challenging, however, because river runoff reflects the net result of multiple interacting processes. Several studies have examined the idea that increased runoff could arise from increased plant water use efficiency in response to greater atmospheric CO₂ availability, via reduced need for stomatal gas exchange and consequent evapotranspirative water losses (Gedney et al., 2006; Betts et al., 2007). However, another modeling study has suggested that this plant physiological response should be compensated by CO₂-stimulated increases in plant biomass, and that in some tropical regions past increases in runoff appear to have been driven largely by changing land use, with climate change of secondary importance (Piao et al., 2007). Another recent modelling study of past discharge records has demonstrated the potential importance of changes in land cover, temperature and irrigation in addition to precipitation and CO₂ (Gerten et al., 2008).

Multi-model ensemble projections extending to time spans of 50–100 years provide the best available indication of where future climatic changes are likely to be most important (Nohara et al., 2006). In general, these model ensembles project that by mid-century mean annual precipitation and runoff will decrease by 10–30% in some dry subtropical and tropical regions and increase by 10–40% in some wet tropical regions (Milly et al., 2005; Bates et al., 2008). For example, mean annual runoff is projected to decrease in southern Africa, tropical Mexico, central America and northeast Brazil, to increase in eastern equatorial Africa and the La Plata River catchment in South America, and to change less in much of the Amazon and Orinoco catchments. Regions subject to monsoonal regimes are likely to become wetter, including southern Asia and northern Australia. Evaporation and evapotranspiration may increase with warming temperatures, and as mentioned before this could counteract the effect of increased precipitation on runoff,

especially in dryland rivers (Dai et al., 2004; Cai & Cowan, 2008). However, climate warming models that project increased evaporation in a warmer world may overemphasise the role of temperature alone as a driver of evaporation (Hobbins et al., 2008).

Despite the uncertainty of model projections, in many tropical rivers the projected changes in discharge over the next 100 years are similar to or greater than the envelope of natural variability over the past 9,000 years, a period of substantial variability driven mainly by changes in solar insolation arising from orbital variations (Aerts et al., 2006). The comparative analysis by Aerts et al. suggests that the Ganges, Mekong, Volta, Congo and Amazon rivers are in this category, whereas the Nile appears less sensitive to future climate change.

One globally consistent projected trend is towards more intense precipitation events (Cook et al., 2008), which has implications for river hydrological regimes and floodplain inundation even if mean annual precipitation and river discharges are unchanged. The frequency and severity of heavy precipitation events are likely to increase in tropical catchments, as are the extent and occurrence of droughts, with both changes projected to take place in some catchments (Bates et al., 2008; Kundzewicz et al., 2008). For rivers, in general, studies have documented how precipitation intensity strongly influences rates of soil erosion and sediment transport into rivers, peak discharges that control many fluvial geomorphological processes, and timing and duration of floodplain inundation (Goudie, 2006). Tropical rivers would behave similarly in these regards, albeit with the most potential for soil erosion in seasonally dry catchments.

Droughts appear to have become more common in recent years, showing some correspondence with elevated sea surface temperatures in tropical regions, although their attribution to climate change remains uncertain (Bates et al., 2008; cf. Marengo et al., 2008; Sheffield & Wood, 2008). Drier parts of the northern subtropics are particularly likely to experience greater seasonal water limitation (Bates et al., 2008). It is important to recognise that seemingly mild droughts in normally humid regions can cause major changes in vegetation and organic carbon stocks, often via increased fire influence (Marengo et al., 2008). For river systems in populated regions with limited water supplies, stronger or more protracted droughts will increase pressure to withdraw

river water for consumptive uses or interbasin diversions (Palmer et al., 2008).

Glacier-fed rivers will temporarily increase in discharge then decrease as the glacial ice becomes diminished. Loss of glacial and snowmelt sources will in some cases impact significant tropical rivers and water supplies downstream, as for example in tropical Andean alpine areas (Bradley et al., 2006) and in rivers arising in the Himalayas (WWF, 2005). Glacial retreat or disappearance may not greatly affect discharge of the larger South American rivers because most of their water originates from more lowland catchments. However, glaciers across the Himalayas and the Qinghai-Tibet Plateau are important sources of water, particularly during low-discharge seasons, to rivers, such as the Yangtze and Yellow in China, the Mekong in Indochina, the Brahmaputra in Bangladesh and the Ganges in India.

Models indicate that tropical cyclones are likely to become more intense in the future (Bates et al., 2008). It remains unclear whether tropical cyclone activity has increased as a consequence of climate change (Goudie, 2006), although there is evidence that tropical cyclones are becoming more severe (Webster et al., 2005). Notably, storm surges associated with coastal storms will increase in impact and area of influence with sea level rise, whether or not the storms become more severe.

Sea level rise is one of the most certain consequences of a warmer climate, but the magnitude and timing are not easily forecast. Projections of sea level rise are being revised in light of the surprisingly accelerated degradation of continental ice sheets, and rises of 40–100 cm over the next century are now being projected (Horton et al., 2008), substantially greater than the 28–42 cm estimates of global models evaluated by the IPCC (2007). Even greater rises cannot be ruled out due to the difficulty in predicting ice sheet behaviour (Hansen, 2007; Steffen et al., 2008; Solomon et al., 2009). In some large river deltas including those of the Mississippi, Nile and Ganges, the effective sea level rise has been considerably exacerbated by land subsidence, which can result from a variety of processes including decreased sediment loads due to upstream impoundments, oxidation of drained organic soils and localised withdrawals of groundwater, oil or gas (Ericson et al., 2006).

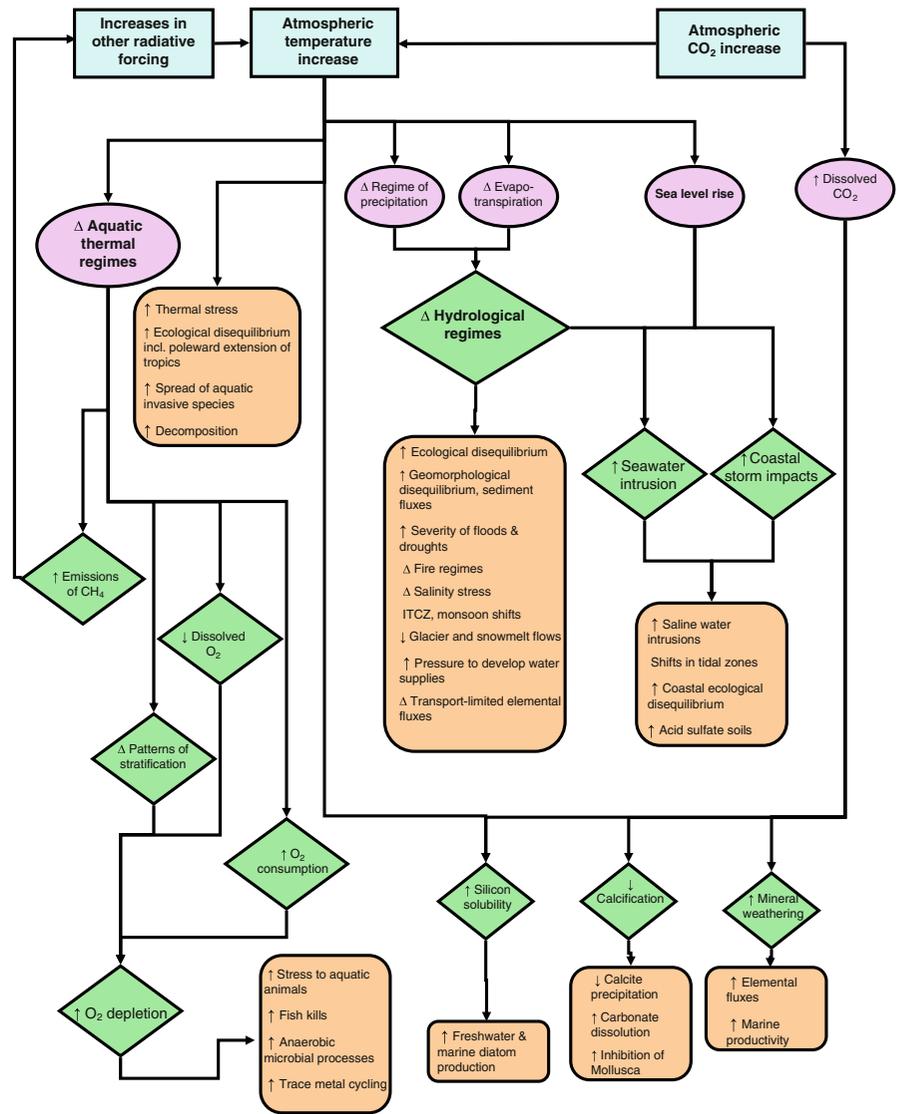
Large-scale changes in terrestrial vegetation may accompany climate change, particularly where

droughts and seasonal water limitation increase to the point where forests are replaced by grasslands, and where the impacts of fires increase. Vegetation water use and land cover have consequences for groundwater recharge and runoff (Li et al., 2007; Costa-Cabral et al., 2007), and may also affect soil erosion and sediment transport into rivers. A substantial fraction of forest in the Amazon catchment may be vulnerable to increased water stress and fires during the dry season, even though total annual precipitation is not projected to change greatly (Bates et al., 2008; Barlow & Peres, 2008). Deforestation in the eastern Amazon has also been linked to decreased plant water use and increased runoff (Chaves et al., 2008), which in turn explain recent increases in discharge of large rivers (Coe et al., 2009). Extensive deforestation could result in regional decreases in precipitation through this feedback, however, and the net balance of these counteracting changes is likely to vary depending on catchment characteristics (Coe et al., 2009). As discussed above, such changes in vegetation would affect plant water use (evapotranspiration), and the water use efficiency of plants is also affected by increasing CO₂ availability. Large-scale changes in vegetation thus represent one of the strongest feedbacks to climate, particularly where changing vegetation produces large changes in carbon sequestration, water use or radiation balance (i.e. albedo), but these feedbacks are complex and incompletely understood.

Conceptual model of biogeochemical implications of climate change

A conceptual model illustrates the major ways in which climate change is hypothesised to affect riverine and floodplain biogeochemistry (Fig. 3). For simplicity, the main driver of global change is depicted as radiative forcing and the resultant global atmospheric temperature increase. Ecosystem-wide increases in air temperature will result in myriad ecological implications, and some would propagate from the terrestrial catchments through hydrological flow paths to affect streams and rivers, in addition to changing land cover and ecosystem processes on seasonally inundated floodplains. Amongst the most notable catchment-wide, direct ecological effects of rising temperatures are increased thermal stress for

Fig. 3 Conceptual model depicting the major ways in which climate change is hypothesised to affect riverine and floodplain biogeochemistry. First-order effects of the increased atmospheric temperature on aquatic ecosystems are depicted as ovals and higher-order effects as diamonds. These effects have ecological and biogeochemical implications that are listed in the boxes. Hydrological regimes encompass the magnitude, timing, duration, frequency and rate of change of key characteristics including water level, discharge and extent of inundation (Poff et al., 1997)



some organisms, a general ecological disequilibrium producing shifts in ecosystem structure including poleward and altitudinal extension of the ranges of some tropical species, and spread of invasive species that exploit new habitats as thermal limitations are reduced. Changes in terrestrial ecosystems are important, but beyond the scope of Fig. 3, which focuses on aquatic biogeochemistry.

Based on my review of the literature, I conclude that the most broadly applicable and probably the most important effects of atmospheric temperature increases on tropical rivers and floodplains entail

changes in aquatic thermal and hydrological regimes and, in low-lying coastal areas, sea level rise, which will interact with the other drivers. Increased dissolved CO₂ in response to higher partial pressures in overlying air is a distinct and possibly significant first-order effect that interacts with higher temperatures to affect mineral weathering and solubility, which in turn control water chemistry at the site of mineral weathering and may affect riverine solute fluxes. Each of these first-order effects and the higher-order effects that follow from them are discussed below.

Changes in thermal regimes

Temperature exerts pervasive effects on many aspects of ecosystem structure and function including biogeochemical processes. Direct impacts of warmer temperatures operate mainly through thermodynamics and the physiological optima of organisms. Thermodynamics drive faster chemical reaction rates at higher temperatures, and many plants and animals increase their growth efficiency (production:biomass ratios) in response to increasing temperature (Talling & Lemoalle, 1998). However, as temperatures climb the point is reached where biotically mediated reactions are subject to biochemical limitations such as enzyme denaturation and loss of membrane functions. Thermal tolerances for organisms are often cited as temperatures at which they no longer function, but their thermal optima are likely well below those tolerances.

The thermal optima of vascular plants, insects and microbes may be of greatest interest in regard to biogeochemical cycles, although biotic changes at all levels of food webs can have significant biogeochemical implications. Thermal optima tend to be narrower for tropical organisms, at least for tropical ectotherms ranging from insects to vertebrates, than they are for equivalent temperate-zone biota, and the thermal response tends to drop sharply from the optimum range to the maximum tolerable temperature (Deutsch et al., 2008). Seasonal minimum temperatures may dictate the ranges of many tropical plants and animals. At high temperatures (e.g. $>30^{\circ}\text{C}$), differences in thermal optima affect competitive dynamics amongst species, and often species diversity begins to drop around 35°C . Hence seemingly modest temperature increases in tropical environments could produce unexpectedly strong reductions or shifts in biotic composition and diversity, with unknown biogeochemical ramifications.

Heterotrophic microbial activity in natural environments tends to increase with increasing temperature, and experimental work with natural wetland soils and sediments supports this generalisation over the temperature range of interest here (i.e. $15\text{--}40^{\circ}\text{C}$). Overall decomposition rates increase with temperature, although the net effect for soil or sediment organic matter pools depends on whether soil moisture and redox status also change, and whether organic inputs change as a result of changes in plant

production (Davidson & Janssens, 2006). Currently, there is not a consensus as to the importance of temperature increases for net ecosystem carbon balances, and most study has focused on upland soils and on northern wetland soils including permafrost. In tropical floodplains subject to seasonal inundation and desiccation, a significant increase in temperature is likely to be accompanied by changes in landscape water balance, the seasonality of soil moisture and inundation, and fire regimes, all factors which may have overriding influences on organic matter pools and fluxes compared to changes in rates of microbial metabolism.

Primary production rates of algae tend to increase with temperature in the range of $15\text{--}30^{\circ}\text{C}$, but may fall sharply above about 35°C , while respiration rates continue to increase (Kirk, 1994; Talling & Lemoalle, 1998). However, in most tropical waters, primary production rates often are more constrained by nutrient limitation than by temperature (Lewis, 1987). Vascular plants with leaves above water are more likely to suffer negative impacts of excessive heating, although plant reaction to overheating has been investigated mainly in terrestrial plants (Berry & Björkman, 1980). Grasses with the C_4 photosynthetic pathway can be important components of aquatic vegetation in tropical floodplains (e.g. Junk, 1997), and are more tolerant of high temperatures than C_3 plants. Thus increasing temperatures may tip the balance of competition in favour of C_4 grasses, which may decrease the nutritional quality of organic matter for consumers, particularly because C_4 grasses tend to have lower nitrogen contents (Gibson, 2009) and provide little support of aquatic food webs (Hamilton et al., 1992; Clapcott & Bunn, 2003).

Anaerobic microbial processes may be responsive to temperature increases. Denitrification seems to be a more effective sink for nitrate in warmer waters, and may contribute to the tendency for nitrogen limitation of primary production in tropical fresh waters and riverine estuaries (Talling & Lemoalle, 1998; Downing et al., 1999). Methanogenesis and iron reduction are two competing processes of anaerobic decomposition of particular importance in tropical floodplains (Roden & Wetzel, 2002; Weber et al., 2006). Both methanogenesis and iron reduction show temperature optima of $32\text{--}41^{\circ}\text{C}$ in anoxic soils from rice paddies (Yao & Conrad, 2000; Fey et al., 2001). Although total methanogenesis increases with

temperature, there is molecular and isotopic evidence for strong shifts in the phylogenetic composition of methanogenic archaea as temperatures climb above 30°C (Fey et al., 2004), and further shifts in methanogen community composition and methanogenic pathways as temperatures climb above 40°C (Fey et al., 2001; Wu et al., 2006; Conrad et al., 2009). Bacterial community structure also changes between 35 and 45°C (Conrad et al., 2009).

Based on this body of study focused especially on methanogenesis, it appears likely that heterotrophic microbial metabolism, including anaerobic processes of key interest in biogeochemistry, will increase in response to higher temperatures. Most estimates of the Q_{10} for aquatic respiration, which refers to the relative increase in rate for a 10°C increase in temperature within the normal temperature range of the environment, and if all else remains unchanged, range between 2 and 3 (Fenchel, 2005). Methanogenesis can have a higher Q_{10} (Roehm, 2005). There may be changes in microbial community composition, but functional redundancy may maintain rates of biogeochemical processes. Thermal stress on the upper end of the temperature range is thus more likely to affect animals and higher plants, while microbes and the processes they mediate seem more resilient within the range of water temperatures that might be experienced.

Tropical wetlands are globally important sources of methane emission to the atmosphere (Denman et al., 2007; Bergamaschi et al., 2007), and hence changes in their contribution can be important as a feedback to climate change. Increased emission of methane by tropical wetlands has been projected, mostly ascribed to higher temperatures, but also related to increased inundation (Gedney et al., 2004; Shindell et al., 2004). However, it remains uncertain whether higher methane production rates will necessarily increase methane emission rates due to the complexity of interactions amongst fermentation, methanogenesis and methane oxidation (Conrad et al., 2009).

An important class of effects of warmer temperatures on shallow tropical waters may be more indirect, involving density stratification and mixing patterns. Diurnal stratification and variable degrees of nocturnal mixing are typical of quiescent water columns that are less than 4–5 m deep, and can be marked even when the water is <1 m deep. The

propensity for diurnal stratification to develop is greater at higher temperatures due to the temperature–density behaviour of water, which results in greater stability changes for a given heat flux as temperatures increase (Lewis, 1987). A diurnally stratified water column intensifies heat accumulation near the surface, and is more likely to result in thermal stress. Increased occurrence and intensity of diurnal stratification enhances the potential for biogeochemical differentiation between surface and bottom waters, which in turn can increase nutrient limitation of surface waters and oxygen depletion of deeper waters. A sequence of days with incomplete nocturnal mixing can result in anoxic waters and lead to fish kills (Talling & Lemoalle, 1998). In tropical lakes, seasonal changes in wind regimes also can be important for stratification and mixing patterns (Talling & Lemoalle, 1998), although wind may be less important as an agent of mixing in shallow and often vegetated waters of floodplains than it is in larger lakes.

Consumption of dissolved O_2 proceeds faster and the solubility of O_2 is lower at warmer temperatures, and these factors combine to make O_2 depletion more likely (Lewis, 1987), with consequences for aquatic animals, the rates and nature of microbial processes and biogeochemical cycles of redox-sensitive elements including many trace metals (Hamilton et al., 1997). Mercury methylation and consequent contamination of food webs may increase with temperature as well (Mauro et al., 1999). The net effect of these changes may be altered species compositions of plants and animals, accompanied by accelerated microbial processes and elemental cycling, with uncertain implications for nutrient limitation and aquatic ecosystem productivity in shallow waters.

Changes in hydrological regimes

The effects of altered hydrological regimes on biogeochemical processes in rivers and floodplains may well prove to be more marked than the effects of warmer water temperatures due to the overriding importance of seasonal inundation patterns in dictating ecological and biogeochemical features of these ecosystems (Junk, 1997; Hamilton, 2008b). Changes in hydrological regimes under a warmer climate begin with the landscape water balance, which

responds to changes in precipitation regimes in combination with higher evapotranspiration at warmer temperatures (see above discussion). Thus magnitude and timing of upland runoff, river discharge and floodplain inundation regimes are all subject to change.

Some major implications of altered hydrological regimes are listed in Fig. 3, although the importance of several of these depends on the setting, and they are not unique to tropical river systems. In addition to ecological disequilibria produced by changes in discharge and flood regimes, geomorphological disequilibria invoked by changes in runoff and river discharge can result in enhanced sediment fluxes from uplands to rivers and between rivers and their floodplains and coastal zones (Ericson et al., 2006; Walling, 2006; Syvitsky et al., 2005). Natural sediment fluxes can be important in nutrient supply as well as in maintaining geomorphologically dynamic environments that often support vegetation in early successional stages. However, enhanced sediment and nutrient fluxes due to changing human land use or climate can result in undesirable geomorphic and ecological disequilibria. Day et al. (2008) discuss implications of changes in inputs of freshwater, sediments and nutrients to coastal zones. Changes in the amount of water moving from upland catchments into river systems usually result in changes in dissolved elemental fluxes as well (Neill et al., 2006), particularly for cases where hydrological transport of solutes in soils and groundwater is the limiting factor (e.g. carbonate mineral dissolution; Raymond et al., 2008).

The vegetation and organic carbon stocks of floodplain ecosystems tend to be sensitive to particularly severe floods or dry periods, which can create new vegetation successional processes (e.g. forest dieback or plant colonisation of emergent sediments). Droughts and fires can rapidly eliminate years of organic matter accumulation in normally saturated soils or sediments, as has recently been documented in Indonesian peatlands (Ballhorn et al., 2009), and may also release methane stored as occluded gas bubbles.

Changes in salinity, tidal influence and marine storms

Salinity is a powerful agent of change in ecological and biogeochemical processes, and in coastal zones,

the boundary between saline and fresh waters usually involves regular or episodic seawater penetration (see below). Inland waters also can become seasonally saline by evaporative concentration, typically accompanied by dramatic shifts in biotic composition and production, sediment-water exchanges and nutrient cycling. Salinisation via evaporative concentration is particularly common in arid and semi-arid climates, but can also occur to some degree in more humid climates where broad shallow pools remain isolated after floodplain inundation (Talling & Lemoalle, 1998). Changes in landscape water balances can change the distribution and timing of salinisation of surface waters (Timms, 1999; Hamilton et al., 2005). In addition, some dryland regions are prone to secondary soil salinisation when land cover changes from woodland to grassland or crops, which alters the soil hydrology such that naturally existing soluble salts are displaced from deeper soils towards the surface (Abrol et al., 1988).

Where large rivers flow into oceans, climate change will have profound implications for biogeochemical processes at the freshwater/seawater interface because gradients of salinity are fundamentally important to ecosystem structure and function (Bianchi, 2007). River deltas reflect the balance between fluvial inputs and marine influences including particularly sea level rise, and modern deltas have formed during the current period of relatively stable sea levels, since sea level rise decelerated in the lower Holocene (Ericson et al., 2006). Day et al. (2008) consider three classes of drivers of importance to coastal wetlands, in general, all of which apply to tropical systems and are potentially affected by climate change: sea level rise, changes in storm frequency and duration and changes in freshwater and sediment inputs. These drivers interact to structure the geomorphology and ecology of coastal wetlands, including freshwater portions of river deltas as well as coastal zones in the area of influence of river discharge and sediment loading, which can extend a considerable distance from large river mouths. Tropical river systems include very extensive coastal deltaic wetlands, such as the deltas of the Amazon, Orinoco and La Plata rivers in South America, the Ganges-Brahmaputra and Irawaddy rivers in Asia and the Gulf of Carpentaria region in northern Australia.

Estuarine and coastal wetlands and floodplains usually exist across freshwater–seawater interfaces,

reflecting a precarious geomorphological and ecological setting developed over several 1,000 years of relatively stable sea levels. The most certain prediction of how climate change will affect ecosystems across these salinity gradients is via sea level rise, although as noted above the projected timing and magnitude of sea level rise remain a topic of debate. Increased intensity of tropical storms is another relatively confident prediction derived from climate change models. These two drivers interact because storm surges will penetrate further inland with higher sea levels. Effective sea level rise from a combination of climate change and land subsidence results in inundation of coastal wetlands, seawater intrusion into surface and groundwater, and increased vulnerability to storm surges (Ericson et al., 2006). Inland migration of these coastal ecosystems will not always be possible in the face of natural geomorphological barriers as well as anthropogenic land use that is often intense along coasts. The floodplains of the Mary River in northern Australia near Darwin are an example where modest changes in topography allowed salinity intrusion via tidal creeks that dramatically altered coastal freshwater wetlands, killing vast stands of paperbark trees (*Melaleuca* spp.; Knighton et al., 1991).

Changes in river hydrological regimes are a complicating factor that can interact with rising sea levels. The complex and interactive effects of storm surges, discharge variability and river channel modifications are exemplified by the Mekong River delta (Wassmann et al., 2004). Decreased discharge (especially during low-discharge periods) worsens the impacts of salinity intrusions. Increased river discharge as a result of climate change could help reduce salinity intrusion and may be associated with higher sediment loads that foster vegetation growth (including particularly mangroves) and land accretion, which in turn may counteract the effects of rising sea levels and provide more protection from storms (Day et al., 2008).

Decomposition rates are lower in fresh waters than brackish waters of comparable hydrology (Craft, 2007), and any seawater influence can elevate the importance of sulphur biogeochemistry including sulphate reduction. Low-lying coastal land that is most subject to flooding by sea level rise may contain former marine sediments known as acid sulphate soils, and when rewetted such sediments can produce

acidic conditions associated with oxidation of sulphide minerals, with negative impacts on freshwater and terrestrial biota (Fitzpatrick & Shand, 2008). Sulphur-linked production of acidity and mobilisation of toxic metals such as Al has been documented in tropical catchments of northern Australia where it is associated with freshwater fish kills (Hart & McKelvie, 1986) as well as negative impacts on coastal marine biota where rivers drain into the Great Barrier Reef ecosystem (Powell & Martens, 2004).

Riverine transport of nutrients to the oceans, which is susceptible to alteration with changes in river hydrological regimes and in the ecosystems they drain, affects marine primary production in coastal waters. Nitrogen delivery is particularly important to coastal marine production (Cotrim da Cunha et al., 2008). Phosphorus, silicon and iron fluxes also affect marine primary production, with effects potentially extending far from river mouths (Subramaniam et al., 2008). Also, deoxygenation of coastal waters is promoted by riverine contributions of nutrients to support phytoplankton growth and of detrital organic carbon, both of which lead to increased respiratory oxygen demands (Cotrim da Cunha et al., 2008).

Changes in mineral dissolution and precipitation

Figure 3 includes several specific chemical weathering processes that are directly influenced by temperature and dissolved CO₂, and are of interest due to their biogeochemical implications. Dissolution of minerals responds to increased temperature as well as to pH (White & Blum, 1995), and in most natural waters pH tends to be inversely proportional to dissolved CO₂ because CO₂ reacts in water to produce carbonic acid.

Chemical weathering of silicate minerals is of particular interest as it represents a long-term sink for atmospheric CO₂, and because it is the source of base cations, alkalinity and dissolved silicate in river waters. Silicate is of particular interest because its availability affects the growth of diatoms, which are ubiquitous and abundant forms of algae in fresh and marine waters. Tropical rivers account for ~70% of global silicon fluxes from land to oceans (Jennerjahn et al., 2006). Silicate mineral dissolution increases with temperature and carbonic acid in water that contacts soils and rocks, and thus the concentrations

of dissolved silicate as well as base cations and alkalinity transported to surface waters may be expected to increase in a warmer and CO₂-enriched climate. However, changes in erosion rates and hydrologic flows through soils and rocks are also likely to be important controls on riverine export of solutes from silicate weathering (Kump et al., 2000; Jennerjahn et al., 2006; Subramanian et al., 2006).

Carbonate mineral weathering is less common in many highly weathered tropical landscapes, but is important to riverine chemistry even where only modest amounts of limestone or dolomite exist, strongly affecting the dissolved inorganic carbon and alkalinity concentrations in river waters. In contrast to silicate minerals, carbonate minerals are less soluble at higher temperatures, but more soluble with increased dissolved CO₂ (Kump et al., 2000), and their solubility is more likely to be transport-limited (i.e. limited by rate of hydrologic flow through soils and ground water reservoirs). Hence, the net impacts of interacting increases in temperature and CO₂ plus accompanying hydrological changes on carbonate mineral weathering are hard to determine.

Subsequent precipitation of calcium carbonate in lakes and marine environments is subject to similar controls, with aquatic metabolism acting as an important regulator of dissolved CO₂ concentrations in productive fresh waters. Secondary carbonate precipitation in surface waters has numerous biogeochemical implications, affecting phosphorus and trace metal cycling (Kelts & Hsü, 1978; Hamilton et al., 2009). Many large tropical river systems in humid climates, including the Amazon, Paraná and Orinoco rivers, carry waters that are dilute in dissolved ions and highly supersaturated with dissolved CO₂, and therefore are not subject to secondary precipitation of calcium carbonate in their freshwater reaches (Kempe, 1982; Oliveira et al., 2010).

Changes in carbonate dissolution and precipitation impact carbon and other biogeochemical cycles directly, but, in addition, they affect calcification by molluscs in fresh waters of rivers and floodplains, where these organisms can play pivotal roles as grazers of phytoplankton and attached algae (Strayer et al., 1999). Relatively acidic fresh waters in some tropical floodplains including a number of rivers in the Amazon River system support low species diversity of molluscs, possibly reflecting the difficulty of biogenic calcification in such waters (Dillon,

2000; Oliveira et al., 2010). In marine environments, the acidifying effect of increased CO₂ overrides the counteracting effect of increasing temperatures, producing potentially severe implications for calcifying organisms including corals and plankton (Raven, 2005).

Conclusions

The prospect of anthropogenically driven global climate change has many potential implications for biogeochemical processes in tropical rivers and floodplains. The most important changes are likely to involve (Fig. 3):

- (1) Aquatic thermal regimes, with implications for thermal optima of plants and animals, rates of microbially mediated biogeochemical transformations, density stratification of water bodies and dissolved oxygen depletion.
- (2) Hydrological regimes of discharge and floodplain inundation, which determine the ecological structure and function of rivers and floodplains and the extent and seasonality of aquatic environments.
- (3) Freshwater–seawater gradients where rivers meet oceans, affecting the distribution of marine, brackish and freshwater environments and the biogeochemical processing of river water reaching the coastal zone.

These changes will, however, be affected by complex human interactions and feedbacks which are difficult to forecast. In river systems that experience decreasing or more variable hydrological regimes, water withdrawals are likely to increase, further exacerbating the hydrologic changes (Alcamo et al., 2007; Kundzewicz et al., 2008). Tropical regions predicted to suffer the greatest water stress for human populations include southern Mexico, northeastern Brazil, parts of northern and southern Africa, and India, driven particularly by increased human demands, with climate change a secondary factor that alleviates increased demand in some cases (Alcamo et al., 2007). Important stressors that can act synergistically with climate change include population increases and urbanisation. These need to be considered in developing strategies for adaptation to climate change (Palmer et al., 2008).

Future research should strive to improve detection of current trends and projection of future changes in catchment and river hydrology, with greater attention to climate feedbacks and human interactions. Limnological research should include sustained monitoring of thermal and mixing regimes not only in large, deep lakes and rivers but also in the shallow and often ephemeral waters of floodplains and wetlands. Thermal optima and responses of microbes (and the processes they mediate), plants and animals in the upper temperature range (e.g. 30–40°C) is a topic that deserves greater attention as well.

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