Article

Climate change and the future of freshwater biodiversity in Europe: a primer for policy-makers

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Abstract

Earth's climate is changing, and by the end of the 21st century in Europe, average temperatures are likely to have risen by at least 2 °C, and more likely 4 °C, with associated effects on patterns of precipitation and the frequency of extreme weather events. Attention among policy-makers is divided about how to minimise the change, how to mitigate its effects, how to maintain the natural resources on which societies depend and how to adapt human societies to the changes. Natural systems are still seen, through a long tradition of conservation management that is largely species-based, as amenable to adaptive management, and biodiversity, mostly perceived as the richness of plant and vertebrate communities, often forms a focus for planning. We argue that prediction of particular species changes will be possible only in a minority of cases but that prediction of trends in general structure and operation of four generic freshwater ecosystems (erosive rivers, depositional floodplain rivers, shallow lakes and deep lakes) in three broad zones of Europe (Mediterranean, Central and Arctic-Boreal) is practicable. Maintenance and rehabilitation of ecological structures and operations will inevitably and incidentally embrace restoration of appropriate levels of species biodiversity. Using expert judgement, based on an extensive literature, we have outlined, primarily for lay policy makers, the pristine features of these systems, their states under current human impacts, how these states are likely to alter with a warming of 2 °C to 4 °C and what might be done to mitigate this. We have avoided technical terms in the interests of communication, and although we have included full referencing as in academic papers, we have eliminated degrees of detail that could confuse broad policy-making.

Keywords: Streams; rivers; floodplains; lakes; temperature; hydrology; diversity; future projection.

Introduction

If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering.

Aldo Leopold (1938)

The climate of Earth is changing rapidly (IPCC, 2007) with human activities mostly responsible for this and many other global changes (Vitousek et al., 1997; Sala et al., 2000). Glaciers are melting, ice covers on lakes form later and melt earlier, and patterns of precipitation and river flow are changing. High floods, heat waves and droughts are becoming more frequent. Rouse et al. (1997) and Schindler (2001) have reviewed the changes in physico-chemical characteristics of fresh waters, but there are also consequences for organisms and ecosystems (Mooij et al., 2005; Jeppesen et al., 2009) with likely feedbacks to the physical processes. Many species are declining (Pimm et al., 1995; Brown et al., 2007; Durance & Ormerod, 2007) whilst exotic species are appearing where they did not occur before (Lodge, 1993; Dukes & Mooney, 1999) and relationships between them are changing, with consequences throughout the ecosystem (Winder & Schindler, 2004).

The stage of the environmental theatre (Hutchinson, 1965) is undergoing a substantial change of scene. The plot of the evolutionary play, a perpetual action of natural selection, competition, predation, immigration and emigration to cope with environmental change, will stay the same, but the future identity of its players, the biodiversity, is very uncertain. Biodiversity has become a widely used word in political agenda. Ecologists used the simpler term 'diversity' until the concept was politicised and this new word perpetrated. It is often viewed, outside professional ecology, as the sole key measure of the state of nature. Particular species are seen as icons, and degradations or improvements are perceived as their exit from, or entry onto, the stage. The perception of professional ecologists, however, is more profound. There are deep questions about what biodiversity means, what its

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significance is in the functioning of the biosphere, and how to measure it. Ultimately, biodiversity is a component of the functioning of ecosystems, but it is the arrangement of the parts that matters more than a simple catalogue of them.

Whilst climate modellers predict the physical states of the water cycle from place to place as temperatures increase, albeit with many uncertainties of detail, ecologists are being asked to predict what will happen to biodiversity in the face of these changes. But there are few simple and general models for biodiversity (Balian et al., 2008) comparable with those for climate and atmospheric chemistry. Living systems embody the complexities of physical systems whilst adding further, much more variable, layers of their own. In this paper we ask how whole freshwater ecosystems might change, in Europe, in response to changes in the greenhouse gas composition of the atmosphere. Our approach has been to examine the issues as a professional group, using expert judgment based on existing experience and information. The discussions were conducted in a three-day workshop in Bristol, UK in July 2007, under the auspices of the EU EUROLIMPACS programme. Our target readership is not our fellow scientists, although we have referenced the paper thoroughly in conformity with our conventions; it is the non-scientists involved in government and policy-making. Increasingly they come from an education and experience that has had less immersion in natural systems (Louv, 2008) than is desirable when the world's major problems are those of its natural environment. To such problems, the more commonly emphasised economic and social problems are subsidiary and derivative. An equable state of the biosphere is the *sine qua non*, without exception, of everything else.

The meaning of biodiversity

For a policy maker, a sophisticated understanding of biodiversity is desirable and thus we discuss some of the important issues about the meaning and measurement of biodiversity before considering the likely effects of climate change on it. To the lay person, biodiversity is an easy concept. It is the number of species of animals, usually meaning charismatic vertebrates, and higher plants. To be big, charismatic, obvious and present is to be significant, but not necessarily most important. An ecologist will point out that there is also a plethora of bacterial and microbial diversity (Torsvik et al., 2002; Weisse, 2006), which is at least as crucial, and probably more so, to the functioning of the planet's chemical cycles; that a species comprises much additional necessary genetic diversity within its apparent uniformity; that there is an important element of relative abundance among the different species that make up communities; and that there are concepts of local diversity (for example, in a particular river), habitat diversity (for example, among rivers) and regional diversity (collective over large areas or distinctive tracts of terrain). These are respectively also called alpha, beta and gamma diversity (Whittaker, 1972).

We decided firstly that there was a greater chance of predicting future regional biodiversity than local biodiversity. The undisturbed communities of individual lakes or rivers certainly have some order in their local biodiversity, but they have a great deal of unexplained variation too. The order comes from the limited number of building processes that influence diversity: dispersal ability, competition, biotic interactions such as grazing or predation, and physical disturbance. The unpredictability comes from random population oscillations that may make a species locally extinct purely by chance, and from the many factors that individually, and often independently, influence each of the building processes in many ways.

If we take a series of communities in a similar category, the invertebrates of small upland streams, or the algae attached to aquatic plants, for example, and use sophisticated statistical methods that correlate environmental conditions with the species present, relationships will emerge, but typically lower than 20 % of the differences will be accounted for, even where a large number of environmental conditions are measured. Any single factor, nutrients for instance, will account for only a few per cent of the variation, and temperature even less.

The unexplained variation may be attributed to unmeasured physico-chemical features and to biological interactions, which are generally not incorporated into the analysis largely because they are too numerous and too subtle for ready measurement. A typical natural water, for example, will have thousands, possibly millions, of different substances dissolved in it, many of them organic compounds, whilst routine analyses cover but a handful of mainly inorganic substances. Biological interactions in turn are equally prolific. Unexplained variation may also come from sampling error. It is rarely possible to sample a community very thoroughly because the intricacies of individual species distributions make this practicably and economically impossible. An implication of this is that the often wide tolerances of many species may mean that effects of climate change over large regions may be obscured by this great complexity.

The richness of undisturbed biological communities will come as a surprise to many policy makers, especially if they are more familiar with agriculture and forestry. In a small European mountain brook in central Europe, the Breitenbach stream, which has been continuously investigated for more than 40 years (Illies, 1975, 1979; Zwick, 1992; Obach et al., 2001), more than 1000 invertebrate animal species have been recorded, but still many more might occur. A typical community might overall have some tens to hundreds of thousands of species, ranging from microorganisms to vertebrates. Where even just potential paired biological interactions among these are considered, the possible number is enormous. There is also a natural turnover in the list of species, brought about by immigration and local extinction. The species list is never constant, and changes in it are influenced by many factors. New species vary in their abilities to reach a site. Insects fly, but the majority not very far. Crawling invertebrates, such as flatworms, seem still to be spreading to fill their potential range following a glaciation that ended 10 000 years ago (Reynoldson, 1983). A gap of only a few hundred metres of different habitat, or a road or field, may deter the spread of riparian forest bats or birds, despite their aerial dexterity.

Naturalists delight in the nuances of local biodiversity, knowing that a particular species may be found here but not there, and recognising the subtleties of patches of environment that are associated with particular animals or plants. Most of these relationships are sensed but not fully explained, although microclimate is often key. The pattern of these small patches will change greatly as climate changes. But because of the numbers of species, the mutual influences they have through their biological interactions, and the inevitable patchiness of their distributions, future local changes are impossible to predict accurately. Regions offer a better target. Regions might be some millions of square kilometres, the size of several European countries combined. Future climate models already make reasonable predictions for this sort of area, and past climatic indicators, for example pollen analysis of sediments and peat, also give consistent patterns for regional diversity (Drescher-Schneider et al., 2007; Miroslaw-Grabowska & Niska, 2007). A region is big enough to smooth out a great deal of local variation. We decided it was practicable to consider Europe in terms of the Mediterranean region, the central land mass, and the Boreal-Arctic zone.

The next issue was which general habitats to consider in such regions. The Water Framework Directive (WFD) (European Council, 2000) requires a typology, or pigeon-holing, of habitats to be drawn up within categories of lakes, rivers, estuaries (transitional areas) and coastal waters, and then the ecological quality of each type determined on a scale whose anchor is a reference state that is essentially pristine ('*no or minimal influence of human activity*'). The habitat types must be defined on fixed characteristics like area, altitude and local geology that may reflect ecological nature, but which are independent of ecological quality. The WFD suggests a few such parameters, but even a few produces hundreds to thousands of combinations. Three sizes of catchment area, three general sorts of geology, three altitude bands and 24 biogeographic regions in Europe produce 648 sorts of rivers, and for lakes, where area and depth are also potentially involved, another order of magnitude ensues. Such a system may be too refined even for the Directive. For predicting the effects of climate change, it is impossibly precise.

We decided that four general categories were sensible: erosive rivers, depositional floodplain rivers, their associated shallow lakes and wetlands, and deep lakes. We recognise, however, that discrete types of any system do not, in reality, occur. There are infinite transitions, or continua, which confound any typology. Considering only very broad

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categories, as we have, is a realistic option, for it enfolds the continua. It also allows inclusion of small bodies of water, such as ponds, that can be excluded from the Directive, despite their overwhelming dominance of the world's freshwater area (Oertli et al., 2002; Downing et al., 2006). Large bodies of water are not more important than small, where either collective area or species richness is concerned.

Measurement of biodiversity

The issue then arose of how to measure biodiversity. Typically, biodiversity studies concentrate on one group of organisms: in fresh waters, usually plants, phytoplankton, zooplankton, macroinvertebrates, fish or birds. They rarely consider the less well-known groups, among them the bacteria, actinomycetes, microfungi, nematodes, harpacticoids, ciliates, benthic algae, and the parasites that are probably much more diverse than the free-living organisms (Torsvik et al., 2002; Balian et al., 2008). It is often assumed that any one group is representative of all groups, that a habitat rich in birds will be rich in ciliates and vice-versa. Where several groups have been studied together, sometimes this is the case (for example, in small farmland ponds, Declerck et al., unpublished manuscript), but often it is not (Green et al., 2002a; Declerck et al., 2005) and where it is, the reasons for a particular diversity may not be the same for different groups (Hawkins & Porter, 2003; Hawkins et al., 2003; Rodrigues & Brooks, 2007). A given habitat will also show seasonal changes and may also vary naturally from year to year, sometimes very strikingly in the Mediterranean region (Bonis et al., 1995; Gafny & Gasith, 1999). Shallow lakes, for example, may switch from a diverse plant-dominated community to a less diverse algal dominated system, with less structure, as a result of human pressures, but they may also do this from year to year as a result of natural fluctuations in weather (Uhlmann, 1980) or water level (van Geest et al., 2005; Beklioglu et al., 2006; Valdovinos et al., 2007) and many organisms may not be common to the two states. Is the biodiversity of such lakes that at any one time or the sum of the several years and states?

Moreover, there is much uncertainty about what constitutes a species, especially in microscopic organisms. There is much variation in fine detail superimposed on what appear to be generally similar cells. Molecular studies increasingly underline the long-realised understanding that almost all individuals within a species are different, and have frequently revealed the existence of several species where only one was previously recognised (Petrusek et al., 2008). They have demonstrated an enormous degree of variation within apparently the same species in adjacent localities (Weider & Hobaek, 2003). Such understanding means that biodiversity will probably always be underestimated where such detailed work is not possible, during routine monitoring surveys, for example. Furthermore, many of the apparent species of small but very abundant invertebrates, particularly nematodes and insects, may not have been described or may be distinguishable only by increasingly fewer experts. Counting species is thus not as simple as it sounds.

One possible resolution of these issues, therefore, is not to consider species or even genera or families of organisms at all but to think in terms of functional diversity (Wilson, 1999; Tilman, 2001; Petchey & Gaston, 2002, 2006; Weithoff, 2003; Hooper et al., 2005). Functional diversity is a measure of the traits that organisms have, or what they do in the ecosystem. Several organisms may share the same group of traits and perhaps functional diversity overcomes the need to recognise species and implies that some species are dispensable if others with similar traits persist. Alas, where powerful statistical techniques have been used to attempt to demonstrate this, it would appear that the ultimate functional units are still the species (Petchey et al., 2007). Groups of traits are unique to species; they are only partly shared. It would seem that there is meaning to the degree of diversity that the very powerful process of natural selection has produced. A system whose parts are tested to destruction in every generation cannot have superfluities. Every cog and wheel has meaning. Yet we can only broadly estimate the list of cogs and wheels in any system.

If functional diversity measures are ultimately still a measure of species diversity, perhaps operational diversity is a possible means to assess the intactness of an ecosystem and a surrogate for species diversity, whilst also telling us more about the ecological quality than a species list alone, however complete, can do. Operational diversity is about processes in a system. The cogs are all there, but in the right relationships and numbers to keep the wheels turning smoothly. If operational diversity is intact, as in a pristine system, we argue that an appropriate species diversity must inevitably be present to support it. Over long periods, natural selection has produced species that make up systems that are operated to mutual benefit for the species that comprise them. A selection process at a higher level among colonisers of a habitat operates similarly to eliminate those species that do not fit into the system (Janzen, 1985; Kawecki & Ebert, 2004; Wilkinson, 2004).

The result is a system that closely fits the local environmental circumstances, maintaining itself and coping with fluctuations through its mechanisms of resistance to change, and of resilience when change enforces a response. The latter may especially rest in its ability to substitute previously minority species (those waiting in the wings in the theatrical analogy) in response to change (Carpenter et al., 1995). A fully operational system is self-maintaining. Systems that require external management for their continuation are damaged systems and the greater the management needed, the greater has been the damage. To be sure, some traditionally managed systems, such as open fens used for grazing or the production of hay, maintain high diversity by preserving a variety of different patches in a small area, and such management has been no detriment locally. The sense here is of big, regional systems that have been over-exploited or seriously disturbed and in which species have been lost or invasive species gained such that management is needed to prevent the loss of others. Such management may be very expensive, whereas self-managing systems cost nothing.

Operational diversity is then a measure of the complexity of the system needed for its independent functioning. It will be reflected in the balance of groups of organisms but not necessarily, beyond a need for trees in a forest, in a list of particular species. It may be manifested by a need for functional groups (guilds) of organisms: primary producers, grazers, different sorts of decomposers and mineralisers, and predators and parasites to police the activities of other guilds. It will require nutrients, but will be most efficient if it uses a limited supply, internally recycled with great parsimony rather than requiring continued outside subsidy. A fully operational system will be big and interconnected with other similar systems through corridors or tracts of other natural systems to ensure the opportunity for immigration of new species that gives resilience, and an area large enough to maintain populations, even of its largest organisms, that do not become inbred and genetically limited. There are many examples that illustrate the mutually beneficial links between different sorts of adjacent systems, manifested especially by flying insects and freely moving fish, birds and mammals (Urabe & Nakano, 1998; Amezaga et al., 2002; Naiman et al., 2002; Knight et al., 2005; Fukui et al., 2006; Klaassen & Nolet, 2007).

Operational diversity would be best expressed in terms of processes (photosynthesis, respiration, carbon storage, nutrient turnover, turnover rates of species, resilience following disturbance) but we do not often have comprehensive and comparable data on these to know what levels are natural or disturbed in specific cases. Paradoxically we therefore have to fall back on a surrogate of broadly operational but taxonomic groups (Murphy et al., 1994), coupled with our experience of working with a variety of systems operating with high, if not pristine, to very low efficiency. Because we have inadequate information on many groups, we decided in this exercise to think in terms of plankton, aquatic plants, benthic macroinvertebrates, fish and birds in making our predictions.

We can therefore now consider the effects of climate change on a matrix of four ecosystems times five broadly operational groups in three regions. Climate change is not a simple on-off switch. It is a progressive process, with a band of possible temperatures predicted for the future century, from perhaps at least a 2 °C increase to maybe 6 °C or more, especially in the Arctic. We decided that we could not be precise about effects at different positions along this gradient but could indicate general trends.

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Determinants of natural biodiversity: existing patterns

There remained two further issues before we could come to a view about how operational freshwater diversity will change in Europe as climate changes. The first was to decide what determines the baseline diversity in systems not disturbed by the powerful influences of a technologically based human society, because change is only absolutely measurable against a fundamental reference. The second was what the counter-effects of mitigation of such a society might be as climate change unfolds. The first of these was the easier to contemplate but was still fraught with difficulty. Diversity clearly shows patterns in particular groups of organisms on Earth. There is often a latitudinal pattern with an increase in species from the pole to the Equator (Hawkins et al., 2003). This has been attributed to the effects of recent glaciation on the one hand, effectively having destroyed habitats so that the polar and boreal zones are in an early recolonisation phase in which species are still returning. Additionally, the longer growing seasons and higher temperatures, allowing more generations and productivity towards the Equator, may have promoted speciation and allowed differentiation of more species. While climatic conditions in some tropical regions have remained relatively steady for some million years, large parts of the boreal zone have been ice-free for only a few thousand years.

There is also a moisture gradient, with endorheic, closed habitats where water leaves only by evaporation, having more extreme salinity and temperature conditions than open, exorheic systems, where the basins have both inflow and outflow of liquid water. Most closed systems in Europe are in the Mediterranean region but cold closed systems occur in the dry Austro-Hungarian plain. Closed systems have specialist species, resilient to drying and salinity, often with life-history stages to survive complete drying out (Cognetti & Maltagliati, 2000).

Actual evapotranspiration rates summarise the combined temperature and moisture gradients. The general trend of biodiversity with evapotranspiration in Europe will be a bell-shaped curve, with low values where evapotranspiration is low because of low temperatures, despite abundant water in the north, and low because of high temperature but extreme shortage of water and higher salinity in the south (Fig. 1).

Then there is a well-established link between nutrient availability and diversity, often shown in terrestrial plant communities (Stevens et al., 2004; Crawley et al., 2005) but also a feature of fresh waters (Dodson et al., 2000; James et al., 2005). Habitats with modest nutrient supplies, above some minimal threshold below which the habitat is so nutrient poor that it is extreme, are associated with high diversity. Conversely, nutrient-enriched conditions favour vigorous, competitive species that exclude smaller, more specialist and less aggressive ones and result in reduced biodiversity (Waide et al., 1999; Mittelbach

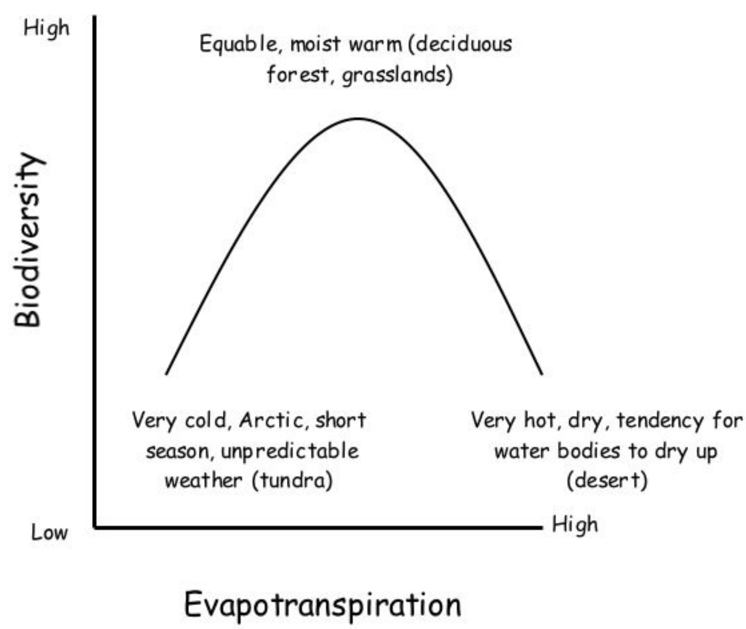

Fig. 1. Relationship between biodiversity (in a wide sense) and evapotranspiration as a general climate indicator.

et al., 2001). This, also, theoretically gives a bell-shaped distribution (Fig. 2) of biodiversity with nutrient availability.

Finally, disturbance influences diversity (Connell, 1978). Considerable disturbance, such as glaciation, leads to extinction. A modest amount of local disturbance leads to a mosaic of sub-habitats that preserve patches at different successional stages and gives comparatively high local diversity (Bonis et al., 1995; Frisch et al., 2006a). No disturbance may lead to the relative uniformity of climax communities, but there is never a complete lack of some sort of disturbance. However, at a regional scale, lack of severe disturbance leads to speciation over long periods, and increasing diversity. In a predictable, little disturbed environment, nutrients and energy are efficiently used by more and more specialist species that develop mechanisms to avoid competition with each other. With time since a major disturbance, such as a glaciation, biodiversity thus increases steadily, tending to, but never quite reaching, a plateau where natural extinction rates are only a fraction smaller than speciation rates (Fig. 3). In the Mediterranean region this process has led to high regional diversity, whilst the salinity effects of high evapotranspiration may give low local diversity.

Seeing these links is easiest in continents that are large and comparatively simple in outline shape so that climatic gradients are steady and latitudinal barriers to movement of organisms, following a disturbance, are absent. Examples are East Asia, the Americas and Africa but there are irregularities even there. Europe is a small and very irregular continent. It has mountain barriers like the Alps, Carpathians and Pyrenees, and marine barriers in the Baltic, North Sea and North Atlantic that cut across climate gradients; in addition, it is a continent riddled with peninsulas and islands that develop their own idiosyncrasies.

Simple climatic gradients therefore do not entirely coincide with the pristine biodiversity patterns in Europe, and the antecedents for species' origin and colonisation have been very different among the main regions. Most of northern Europe was covered by ice sheets up to 10 000 years ago; almost no distinctive new species have developed there as a result of recent evolutionary processes (although there is much evidence of speciation in progress (Ferguson & Taggart, 1991; Sandlund et al., 1992; Weider & Hobaek, 2000)), and almost all species occurring have immigrated in the last 10 000 years. Usually these have been flexible, widely distributed species, capable of coping with a variety of habitat conditions, with high dispersal rates. During the ice ages, central Europe was located between the main ice masses covering northern Europe and the Alps. Similar to northern Europe, only very few species have their origin in central Europe, but immigration from refuges in the Mediterranean zone was simpler, since distances were relatively short and a variety of habitats developed shortly after the ice age. In the Mediterranean zone many species survived the ice ages in refuges, often radiating to further species and subspecies as a

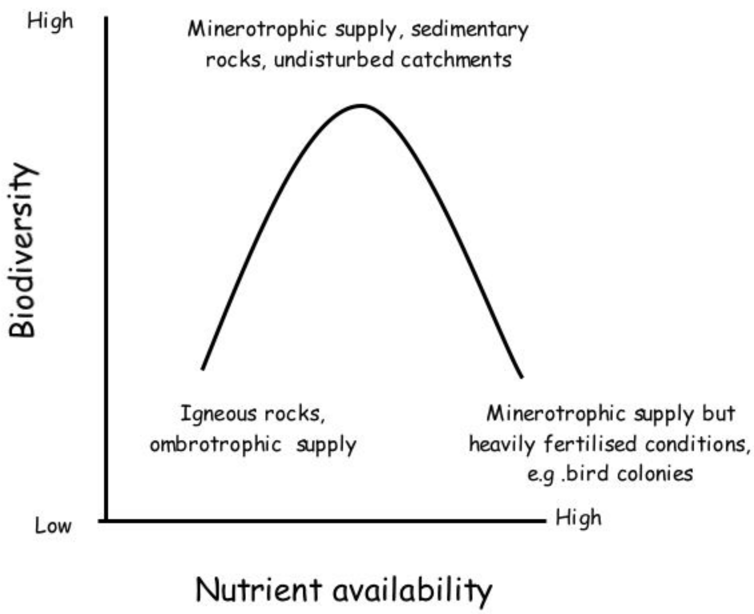

Fig. 2. Relationship between biodiversity (in a wide sense) and key nutrient availability (largely N and P). Ombrotrophic refers to supply by direct rainfall; minerotrophic refers to supply after percolation of the rainwater through the ground.

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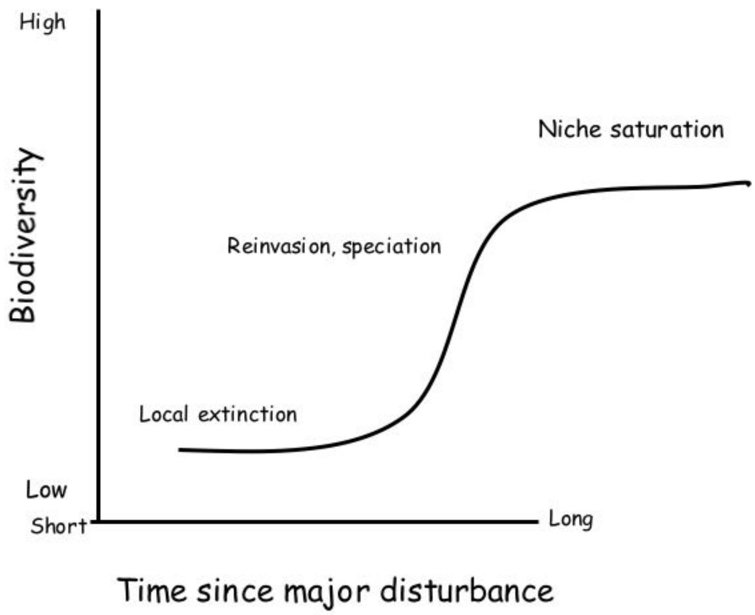

Fig. 3. General relationship between biodiversity (in a wide sense) and time since a major disruption or disturbance as a result of a combination of processes including invasion and speciation.

result of isolation (Cosswig, 1955; Pauls et al., 2006). Many of these species have a restricted range and have not (yet) managed to colonise other parts of Europe. Most groups of plants and animals are thus characterised by a high number of often specialised and endemic species in the Mediterranean, and a low number of more generalist species in northern Europe, with central Europe being intermediate. This general pattern in biodiversity is a result of ice disturbance, rather than present climatic conditions, although the two phenomena are obviously linked.

Analoguesia

Since existing climatic gradients in Europe seem to be less suited to explain current biodiversity patterns, confounded as they are by major past events, we needed a conceptual model to predict future changes and so invented a regular continent we called Analoguesia. Three main axes define its environment. The first is a climatic one, summarised as evapotranspiration rate, which effectively combines the influences of temperature and water availability and incorporates rising salinity in endorheic areas. The second is a gradient from ombrotrophic (rain-fed nutrient) conditions to minerotrophic (ground and soil-water fed nutrient) conditions, reflecting not only local geology but its interaction with climate. Poorly weathered igneous rocks have waters dominated by rainwater chemistry; weathering of more soluble sedimentary rocks increases the ionic concentrations substantially, but can be overridden in very wet areas. The surface vegetation even on limestone becomes rainwater-dominated if precipitation is high enough, as in western Ireland. There is a general relationship between lower nutrient availability in ombrotrophic conditions and higher in minerotrophic conditions.

The third axis is time elapsed since a major disturbance, major being one with powerful effects and regional coverage, such as an ice age or extensive volcanic activity. Combinations of the relationships shown in Figs 1, 2 & 3 gave the three dimensional picture of Fig. 4 for Analoguesia and allowed us to envisage how climate change might impact on this picture. For example, trends can be traced as evapotranspiration changes, as habitats become more minerotrophic when evaporation rates increase and ombrotrophism becomes less prominent, and as regional droughts and, in some cases, regional flooding cause major disturbances.

Mitigation

The second issue of possible mitigation by human societies, as temperatures increase in future, is much more speculative. Humans have already greatly altered natural patterns of biodiversity (Vitousek et al., 1997; Cumming, 2007). Traditional peoples have probably influenced biodiversity progressively ever since it was learnt that fire could determine the local vegetation, the nature of hunting habitats and vulnerability of prey. Technological societies,

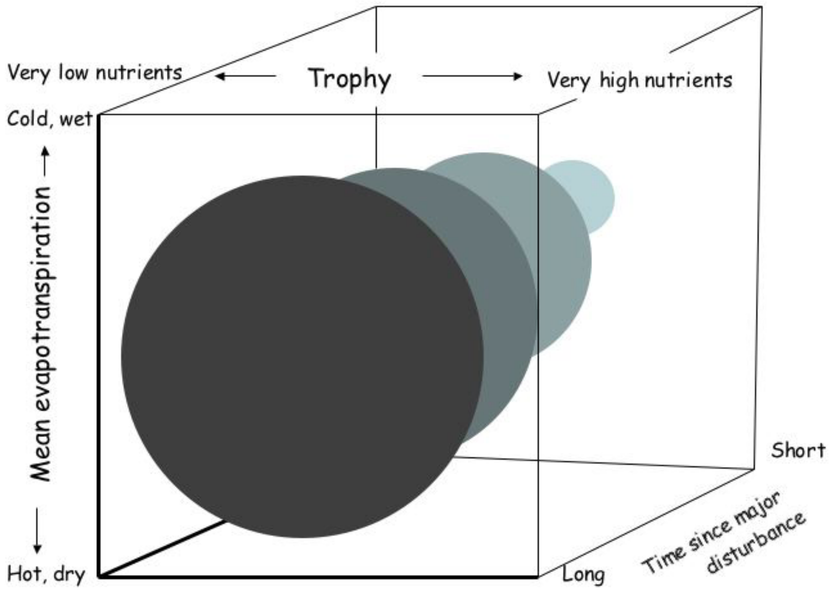

Fig. 4. Combined effects of climate, nutrient availability and disturbance in determining biodiversity (in a wide sense) in a hypothetical regular continent, Analoguesia, in which there are no latitudinal barriers to movement of organisms. The greater the depth of shading, the greater the biodiversity.

however, now dominate biodiversity and there can be almost nowhere on Earth that their influence is not felt. In Europe, the concept of even a nearly pristine habitat, the gold standard of high ecological quality for the Water Framework Directive, is that of the Holy Grail. Beyond a local increase in the diversity of patches of land owing to light, traditional agricultural management, where this still persists, the influence of humans on biodiversity is usually very negative. Acidification, eutrophication, toxic pollution, urban development, river engineering and drainage all impoverish habitats, and deliberate or accidental introductions of species usually have the same effect through competitive mechanisms that displace native species (Lodge, 1993; Lodge et al., 1998; Dukes & Mooney, 1999; Sala et al., 2000).

A great deal of uncertainty as to the impacts of climate change on biodiversity hinges on how human activities might change in order to attempt to mitigate its effects. Mitigation might include industrial, agricultural, conservation and social changes, all of them often powerful determinants of current biodiversity. New methods of generating energy such as tidal generation could have major effects on estuaries and the lowland floodplain sections of rivers. Expansion in hydroelectric power generation would effectively block the runs of migratory fish where these still occur, despite the incorporation of fish ladders and passes, which are often not very efficient. Reservoirs also cause release of methane, a potent greenhouse gas, as the former terrestrial soils are waterlogged. Generation of electricity by biomass burning could turn huge swathes of land into monocultures of willow. These might be less heavily fertilised than food crops and hence reduce the nutrient pollution of fresh waters, but the reverse could be the case if herbaceous crops, like sugar cane or rapeseed, were used. Changes in agriculture will be inevitable as already hot environments become deserted, environmental refugees move polewards, import of food becomes restricted and more home-grown food is required. Intensive agriculture and dense settlement are the two central destroyers of biodiversity.

Introduced species might become an even more severe problem. There is often legislation against uncontrolled introductions but if commercially or recreationally important species disappear there may be a tendency to introduce replacements irrespective of their legality. Introduction of one species generally brings in many others, unseen stowaways in water, or attached to the intended species. Future agriculture and aquaculture, demanding higher production to compensate for loss of farmland in lower latitudes, might also make greater use of genetically modified species, with potentially similar risks to those that come from introduced species.

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Therefore our, and indeed anyone's, prediction of the future biodiversity can only be very general. Elaboration of apparently objective 'horizon scanning' techniques, formalised into ostensible credibility by elaborate computer models, has little meaning if the basic information is very fuzzy. Confinement of predictions to operational diversity on a very broad scale is as honest an approach as is possible.

Scenarios

Bearing all these things in mind, we have condensed our predictions into scenarios. We have first briefly reconstructed a scenario for pristine (high quality) conditions for each of our four habitat types. Our impression of much current policy-making is that there is very little concept of what pristine conditions were like. With every successive generation of policy-makers, their experience, based on growing up in a world being damaged at unprecedented rates, becomes more and more separated from ecological reality. Secondly, we have indicated how this pristine scenario has changed with current human impacts. We have then projected onto this a temperature change of about 2 °C to 4 °C, with associated hydrological changes as predicted by the IPCC (2007). It seems unlikely now that we will avoid a 2 °C rise and with current political and social resistance to making severe enough changes in ways of life everywhere, a much greater increase is likely in the foreseeable future. Our use of three broad zones of Europe – the boreal and polar, central, and Mediterranean – is coarse, but with four main habitats, three zones, five biological components and three scenarios, we have still had to juggle a total of 180 different balls and this gives some insight into the practical difficulty of attempting prediction in any greater detail. Lastly, we have indicated what might be done to mitigate the likely changes to our already modified systems, so as to help maintain their ecological operation by retaining a characteristic biodiversity. For those few systems, in the remote areas of the continent, where relatively undamaged systems still remain, the only prescription can be to do nothing other than, if possible, extend their areas, particularly in a north-south direction. The essence of a pristine system is that it manages itself and any human intervention is most unlikely to be beneficial.

Change in erosive river systems

A river forms a continuum, along which many things systematically change: discharge, current, sediment load, temperature and food sources as well as species composition. 'Erosive river systems' include small and medium-sized rivers, largely located in hilly and mountainous regions, where the net effect of water flow is to abrade material from the bed and move it downstream. There is a smooth transition to depositional rivers, with the transition zone being particularly rich in habitats and species.

Pristine erosive river systems have wild waters cascading in a single channel through narrow valleys, especially in spring when snow melts from the uplands. Though tundra-bounded at their highest altitudes and latitudes, they become dominated by forested riparian (bankside) zones southwards and towards sea level. The forest and the stream are one system, for the main energy source for the aquatic community is the terrestrial litter blown or falling into the water, and held back by rocks and woody forest debris that also naturally falls in. Invertebrate groups, the leaf shredders and wood borers, the filter-collectors and the deposit feeders, process this litter, the former two groups breaking it down to particles that the latter two can gather. As the river widens, rocks in its unshaded centre become colonised by algae and mosses that are fed upon by invertebrates scraping the surfaces. In turn the invertebrate processors are eaten by invertebrate, fish and bird predators.

Nutrients are scarce, for pristine forest systems have powerful conservation mechanisms that limit losses from their soils, but supplemental sources come from the ocean through migratory salmonid fish, their carcasses after spawning, and the excreta of bears that feed upon them (Naiman et al., 2002). The latter secondarily fertilise the trees of the immediate riparian zone. The debris of these trees, falling into the water, retains the carcasses, and the nutrients that eventually decompose from them, within the river stretch. Aerial insects trapped at the water surface provide food for fish whilst riparian forest spiders, beetles, bats and birds may depend on the emergence of stream insects (Kato et al., 2003; Fukui et al., 2006). In the more open stretches, thickets of willow may form, the food of moose and other deer, whose numbers may be controlled by wolves that are essential to maintenance of the plant and bird diversity in the river corridor (Ripple & Beschta, 2004a,b; Beschta & Ripple, 2008). High flows move rocky debris around, and gravel and sand bars separate the braids of what becomes a structurally complex system, with successions to woodlands of poplar, willow and alder on the islands in the stream. In Mediterranean regions, similar systems show their particular characteristics in generally lower, but flashier flows, more open woodlands and reduction of the stream channel in the hot dry summers (Acuña et al., 2005).

Like all other aquatic ecosystems in Europe, erosive river systems have already been changed by many impacts. There have been large amounts of acidity delivered in rain and snow, but many small streams have not been so severely polluted in other ways, so a comparatively high share of invertebrate species has been conserved. However, physical alterations in their catchments affect almost all European streams and rivers, and disrupt the river continuum and the links between the stream and its terrestrial surroundings. Most of the rivers, even in Scandinavia, have been straightened and the channels cleared of woody debris and large rocks to ease the transport of timber from upstream logging to the coastal sawmills (Törnlund & Östlund, 2002), or they have been dammed for hydroelectric generation. Intact medium-sized rivers can only now be seen in northern Russia and in a few National Parks to the south, although the latter are largely depleted of their large mammals. The typical central European erosive river is already hugely engineered to control flows, and has several barrages for water storage, flood control or hydroelectric generation. Its riparian zone may still be wooded, but the forest is often a token fringe, or consists of exotic, fast-growing planted conifers. The interactions with large mammals have been lost, as have been the former prodigious movements of the Atlantic salmon. Development of the catchments as pastureland, ski slopes (Molles & Gosz, 1980) and towns has increased nutrient flows, leading to large growths of filamentous algae on rocks and a change in the macroinvertebrate community from detritivores towards herbivores. Dams have also changed downstream features (Palmer et al., 2008), with a loss of leaf material and shredders, but with filter collectors often abundant below them, feeding on plankton from the released reservoir water. Control of flows has led to much more build up of sediments in semi-permanent beds and a simpler, less dynamic geomorphological structure. Woody debris is scarce, for modern forestry turns everything into a commercial resource and is even depriving some systems of essential calcium (Jeziorski et al., 2008). But the nutrient parsimony of the former system is generally replaced by a nutrient surplus that leads to loss of biodiversity and sometimes dense beds of plants that must be regularly cut to prevent summer flooding of a riparian zone that is now agricultural or built upon.

Many of these impacts lead to an upstream shift of the former characteristics of the river continuum. Removal of riparian vegetation increases water temperatures to values typical for downstream regions; organic pollution and eutrophication reduce the oxygen content of small streams to that typically found in medium-sized rivers. Processes and biota change accordingly. In terms of temperature, oxygen and food resources, the majority of erosive river sections today resemble the original state of their downstream reaches, but at the same time lack characteristic features of larger rivers, such as the high discharge.

Climate change will worsen this situation by further increasing water temperatures and associated features. It will contribute to a general upstream movement of river zones, particularly obliterating species bound to small streams and springs, which cannot move further upstream. Most fish of small rivers, especially the salmonids, are cool- or cold-adapted, and we may expect their loss with replacement by warm water cyprinids (coarse fish) where the system is large enough and still not dammed from its lowland reaches to prevent movement. Changes in hydrology that lead to reduced summer rainfall may promote further damming for water supply and storage and further disruption. Extreme rainfall events, which are

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predicted to increase in frequency, will more often re-set the structure of the system. Summer droughts may reduce flows very greatly and this will be especially so in the Mediterranean zone, where many rivers will be completely dry for large parts of the summer. Rivers process organic matter released by human societies and in the past had to cope with raw sewage. In general the extremes of that problem, and the consequent huge reductions in biodiversity among fish and invertebrates, have largely passed, but a great deal of organic matter is still discharged. In the reduced flows of warmer water in summer this will cause increased deoxygenation, threatening animal communities and the ability of the river to deal with urban and agricultural wastes. Arctic streams will be particularly vulnerable (Prowse et al., 2006) for temperatures are predicted to rise much more than in central Europe. Arctic fish communities are poor in species so that the loss of even a single species may mean a halving of the fish diversity. Declines in Arctic charr have already been noted and published for one temperate lake (Winfield et al., 2008).

Mitigation of the effects of climate change should be combined with measures to improve ecological quality under the Water Framework Directive. Hitherto, improvements in water quality in English streams have sometimes masked climate-induced changes (Durance & Ormerod, 2009) but this will not indefinitely be the case. The lessons to be learned from intact systems are that connectivity, both along the course and with the terrestrial surroundings, reduced nutrient inputs and increased afforestation with native species (which will shade the stream as well as provide its energy source) are the three primary approaches to combat the effects of eutrophication, organic pollution, acidification, habitat degradation and climate change. Removal of dams may be impracticable, but ensurance of greater compensation flows than those currently allowed, and better design of fish passes that allow fish to move both upstream and downstream of the dam, will help. Above all, existing measures to combat existing problems, such as acidification, must be continued, even increased. Climate change does not replace existing problems; generally it will worsen them.

Depositional rivers

Even more than their erosive reaches, the lower floodplain courses of rivers have already been seriously damaged by human activities (Postel et al., 1996) so that almost no completely intact depositional floodplain rivers still exist in Europe. They develop naturally where the catchment has reached a size that the amount of water entering at peak flows cannot be accommodated by the single or few channels that cope with summer flows. The central channel meanders to increase its capacity but the flows that occur in winter and spring will spill onto a wider channel, the floodplain. The floodplain varies in width depending on the size of the river and its catchment, and therefore its outer reaches may be dry in some years, giving the wrong perception that this is dry land, sometimes flooded, rather than the reality of a sometimes-dry river bed. At least one flood pulse will be experienced every year in an intact floodplain system. It will shift enormous quantities of silt and other sediment from upstream and will create a series of changing features on the floodplain: levees, backwater lagoons, ox-bow lakes where meanders are cut off, and a series of vegetation zones stretching outwards from a permanent swamp close to the summer channel to progressively less wet woodlands and grasslands at the floodplain fringes (Maltby et al., 1996; Steiger et al., 2005). Large European rivers, like the Rhine, Vistula or Danube, historically had floodplains several kilometres wide, which formed a mosaic of main and abandoned channels, side arms, sand bars, and floodplain forest patches in many successional stages.

In its pristine state, this complex structure harboured animals that fed on the emergent swamp vegetation, woody debris from the swamp forest, and organic deposits brought from upstream or derived from the high productivity of the swamps. The summer channel acquired some lake-like characteristics, developing first a zooplankton community in the turbid water, and sometimes a phytoplankton community where water was retained long enough for the community not to be washed downstream (Reynolds, 2000; Amoros & Bornette, 2002). In the swamp lagoons and ox bow lakes, the water cleared and a lagoon community developed so that the floodplain as a whole acquired a considerable diversity. At low water there was much interaction with the forests along the floodplain margins as wild horses and ungulates moved in to graze on the lush grasslands, followed by their predators. There was a rich community of water birds. Fish migrated both up and down river and outwards from the summer channel into the swamps to feed and spawn as water levels increased in spring. Many traditional human cultures have used the rhythm of water level change to support a subsistence based on fishing in the wetter period and temporary cultivation or grazing in the drier period.

Much of this structure and function has been destroyed in European floodplains through the arrant misperception that the floodplain is land that needs protection through artificial levees and barriers, so that it can be built upon or farmed. Floodplain soils are very fertile when drained until their peats oxidise to an infertile acidity. The river system has therefore often been reduced to the summer channel, deepened and often straightened to hasten the removal of water downstream. Water is pumped into it from the former floodplain through a series of straight ditches. The level of the plain will often have sunk to below that of the river as the former organic soils have oxidised and even the inorganic soils have shrunk on drying. The pumped water is often of poor quality, with high nutrient levels and traces of biocides used in the agriculture that develops. Moreover, the loss of water storage on the floodplain will have led to greater rates of passage of water downstream and a progressive need for more elaborate flood control in the reaches closer to the sea. Once there has been a start to floodplain destruction it becomes unstoppable until no floodplain at all is left and the river is a simple, deepened canal of very little value in the preservation of floodplain biodiversity, flood-control or water purification services. Its key characteristic, the patchy fluctuating mosaic of terrestrial and aquatic habitats, has been lost. The channel itself will continue to act as a habitat for aquatic organisms. Many large rivers were, however, so severely polluted in the 20th century that there was almost the complete disappearance of organisms other than bacteria. After pollution was reduced, the plants and animals that first colonised the competition-free space were often invasive species, so that the communities do not at all resemble the original state (Gherardi, 2007).

We do not expect a great deal of further decline in biodiversity that will be consequent on warming of floodplains in the central European and Mediterranean zones. They have already been comprehensively wrecked. For the few remaining floodplain sections, warming might bring changes to the community of migratory birds (Sutherland, 1998) and to the dominant swamp plants. Egrets, formerly only occasional in the UK, are now becoming common (Combridge & Parr, 1992) as temperatures rise, and first bred in the UK in 1995. More black-winged stilts arrive in the UK from the Mediterranean in warm years (Figuerola, 2007). Warming will reduce oxygen concentrations in the backwaters and swamps, but swamp waters are naturally deficient in oxygen and communities able to cope with this have developed, usually by adopting some form of air rather than gill breathing. The expected rise in temperature will only modestly change this situation.

What may be a far more prominent consequence, however, is the expected change in hydrology and the frequency of extreme events (Michener et al., 1997). Storms have already led to reclamation of part of the Mississippi floodplain at New Orleans and in 2007 overtopped many existing flood defences in the UK, India and China. The response to this has been to contemplate even larger defences. Bigger flood defences will probably not decrease biodiversity greatly for there is comparatively little left in severely engineered systems. A more sensible long-term approach, however, would be to reconstitute the floodplains to their fullest extent, progressively from the upstream reaches to the lower; this would be accompanied by greatly enhanced biodiversity and better downstream flood protection for cities and towns.

In the Arctic there will be serious damage. Here, especially in the big river deltas of northern Scandinavia and Russia, there are still extensive areas of floodplain. Floods are to some extent dependent on ice dams that form as the rivers melt northwards in spring, and the permafrost system provides freeze-thaw mechanisms that give rise to millions of small lakes and lagoons. As temperatures

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increase, permafrost melts and these features will be progressively lost in a more amorphous swampy landscape, possibly lacking the isolated small bodies of water that currently support often very different communities within short distances (Hobaek & Weider, 1999). Roads and railways will be undermined, productivity of blackfly and mosquitoes will increase and existing economic activities in these regions may have to be abandoned.

Shallow lakes

Shallow lakes, in the sense used here, are those where the predominant primary production comes from algal and submerged plant communities associated with the bottom, rather than from the phytoplankton (Moss et al., 1996; Lachavanne & Juge, 1997). In practice this means lakes with a mean depth less than about 3 m. In their pristine state, such lakes are rich in biodiversity, except sometimes in highly peaty regions where the water is stained deep brown and light penetration is impeded. Otherwise, a community of perhaps 10–30 submerged macrophyte species (James et al., 2005) supports a diverse periphyton and plant-associated invertebrates (Kornijow et al., 1990). There are many fish and water birds. A plankton community is also present, but dominance by individual phytoplankton species is avoided through grazing by the zooplankters that find refuge against their fish predators within the plant beds. The water remains clear as a result, even at artificially high nutrient concentrations, although in the pristine state, with a catchment covered by natural vegetation, nutrient inputs will be low. In ponds, which also come within this category, amphibians will flourish where fish are absent (fish eat tadpoles), and natural drying out of some small ponds will also support a diverse community of unusual invertebrates capable of aestivating under such conditions (Jakob et al., 2003). Mediterranean shallow lakes that dry out in summer may be individually less diverse than those in central Europe for they are strongly limited by changes in salinity (Green et al., 2002a, 2005; Frisch et al., 2006a,b; Beklioglu & Tan, 2008) but support a specialist fauna derived from a high regional diversity well adapted to that (Giudicelli & Thierry, 1998; Bazzanti et al., 1996; Boix et al., 2001). Permanent Mediterranean lakes will be very diverse and rich in fish although sparse in the salinity-intolerant Cladocera, leading to reduced zooplankton grazing and higher phytoplankton densities. Natural changes in water level lead to the presence of extensive plant beds in Lake Kinneret in Israel in some (low water) years and complete absence when levels are higher (Gafny & Gasith, 1999).

Human activities have frequently switched these systems to a turbid state lacking plants and with reduced diversity (Irvine et al., 1989; Scheffer et al., 1993; Davidson et al., 2005), although the process can also occur naturally following different winter weather conditions (Uhlmann, 1980) or weather-induced changes in water level (Blindow et al., 1993). A combination of increased nutrient loading and specific impacts that destroy the plants (severe cutting, herbicides, introduction of exotic grazing birds such as Canada geese, fish such as common carp, or invertebrates such as Louisiana red swamp crayfish (Rodriguez et al., 2003)) or those that disrupt the mechanisms that maintain the water clarity (for example, toxicity to zooplankton through pesticide residues, increased salinity or heavy metals) is responsible. There has been considerable effort in Europe in recent decades to restore these systems because of their conservation and biodiversity importance (Moss et al., 1996; Jeppesen et al., 1999, 2005).

Warming may counteract these efforts. Warming may enhance the symptoms of eutrophication by increasing the rate of release of phosphorus from sediments (McKee et al., 2003), increasing phytoplankton growth rates (van Donk & Kilham, 1990; Reynolds, 1997; Howard & Easthope, 2002) and encouraging the growth of exotic plant species that displace native species (McKee et al., 2002), not least floating species (Feuchtmayr et al., 2009), some of them such as *Salvinia* and *Pistia* spp. causing major problems. In Sweden, a prolonged growing season appears to be favouring the invasion of a mucilaginous alga, *Gonyostomum semen*, which dominates the phytoplankton biomass with reductions in overall diversity. Warming will decrease oxygen concentrations as a result of purely physical relationships at least, but disproportionately from increased biological activity, leading to changed fish breeding behaviour and fish kills of many species. The piscivorous Northern pike (*Esox lucius*) is expected to show some of the most severe decreases (Reist et al., 2006). Few fish will easily survive a very hot summer in a shallow lake, but the introduced, rather damaging common carp (*Cyprinus carpio*) will, and indeed may breed more effectively in the cooler parts of Europe than it does at present. The native tench (*Tinca tinca*) and crucian carp (*Carassius carassius*) may also thrive. In addition, there may be life history changes, leading to dominance of small, fast reproducing species and individuals, with major consequences for abundance and diversity of lower trophic levels (Meerhoff et al., 2007; Jeppesen et al., 2009).

Loss of native fish may encourage anglers to distribute these fish more widely and perhaps illegally, and bring in other species with the intentions of sport rather than balanced biodiversity. Small ponds may suffer more frequent drying out in warmer summers and in the Mediterranean zone many will disappear (Blondel & Aronson, 1999). Those shallow Mediterranean lakes that persist, already stressed by variable and high salinity, will become more saline, more extreme environments, with reduced diversity (Cognetti & Maltagliati, 2000; Nielsen et al., 2003; Brucet et al., 2005; Green et al., 2005, Beklioglu et al., 2007; Boix et al., 2008). With reduced water levels, the former open water of Lake Chameiditida in Greece has become dominated by a floating raft of emergent plants (mostly *Typha*) since the 1970s. Many amphibians will become locally, perhaps regionally extinct. Small positives might include reduced nutrient loading from decreased precipitation, but greater release of nutrients from the sediments and increased frequency of complete drying out will cancel any such advantage (Beklioglu & Tan, 2008; Jeppesen et al., 2009).

Shallow lakes have suffered greatly from human activities and restoration has involved a considerable effort to reduce phosphorus loads (Cooke et al., 2005), remove damaging fish communities (van Donk et al., 1990; Hansson et al., 1998; Mehner et al., 2002) and limit ingress of toxic pollutants. Mitigation against warming can only mean a redoubled effort in these measures but will be confounded by a potentially increased intensification of agriculture for local food or biomass production, a spread of exotic species that inevitably have been brought in from the warmer regions and which will therefore thrive, and misguided and largely uncoordinated attempts to maintain the fish stocks demanded by the more competitive of anglers.

Lakes have the problem (and sometimes advantage) of greater isolation than river systems and although flying insects will readily colonise a new lake, migration of species from the south to replace those that do not survive warming will be impeded by isolation (Reist et al., 2006). Individual populations may become extinct in any case if migration is too limited and the residual populations lack genes that would allow them to adjust to climate change. Nonetheless, birds are major vectors of both invertebrates and plants (Green et al., 2002b; Green & Figuerola, 2005; Frisch et al., 2007) and migratory birds may become very important in restocking biota depleted by warming. The situation for fish and amphibia is dire, however, where major barriers of mountain or sea intervene.

The prognosis for the distal islands of Europe such as Iceland, the Faeroes, Ireland and the United Kingdom, is especially bad. Pressures to introduce species deliberately will be greater than on the mainland and since there is a high chance of other species (associated algae and invertebrates) being introduced with the intended fish and plant introductions, there is a risk that although biodiversity might be maintained in terms of species richness, there will be major problems in the structure of the communities that persist. Mooij et al. (2005) believe that warming will exacerbate the loss of submerged plant communities. Mescosm experiments (McKee et al., 2002; Feuchtmayr et al., 2009) do not support this but suggest a major increase in floating plant communities and inevitable fish kills. Comparative analyses of lakes in Europe, Florida and Uruguay, however, indicate an increase in many symptoms of eutrophication, even if plants are present, and loss of water clarity (Jeppesen et al., 2007, Meerhoff et al., 2007). A secondary spread of common carp could prove devastating to the plants, proving Mooij et al. (2005) indirectly correct.

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Deep lakes

Deep lakes are not sharply distinct from shallow lakes, but in general their productivity is dominated by communities of phytoplankton rather than by bottom-living communities of submerged plants and associated algae. They often acquire distinct layers of floating warmer water (epilimnia) and colder denser water (hypolimnia) during the summer. In Europe, deep lakes are widespread in upland regions or regions of poorly weathered rock. In their pristine states they have very low nutrient loadings and clear waters, are dominated by a sparse plankton, and often by fish that remain planktivorous even in adulthood. Deep lakes have a narrow littoral zone, often as rich in species as shallow lakes, but whose coverage of the bottom is much limited by the depth of the basin. Large size may give an increased overall richness not least because the existence of sheltered bays and exposed shores in the same water body leads to a variety of inshore communities. Dependent on absolute depth and continentality, which increases the stability of the layering because of higher surface temperatures, hypolimnia may be naturally poor in oxygen or even anaerobic, but typically are big enough to retain a substantial oxygen store, for example in the large sub-alpine lakes. The deeper waters may provide summer refuges for cold-adapted fish such as the coregonids and salmonids, and the open waters provide hunting grounds for birds like fish eagles, ospreys, mergansers and divers that shun smaller, shallower lakes and are part of the pelagic food web.

Development of settlements on desirable shorelines is often a greater source of nutrients than agriculture, in contrast to the situation for many shallow lakes in the lowlands. Eutrophication leads to greater deoxygenation of hypolimnia, to blooms (Ibelings et al., 2003) (in the strict sense of cyanobacterial populations that migrate within the water column sometimes to form a surface scum – the bloom), and potentially to elimination of cold-water fish species that require high oxygen concentrations and which previously found cool oxygenated refuges in summer in the hypolimnion. Acidification tends to eliminate many animal species through damage to gill and other membranes and interference with reproduction, and to bring about less diverse plant communities as *Sphagnum* comes to predominate. Precipitation of phosphorus by aluminium mobilised from the catchment and removal of bicarbonate by reduced pH may result in a greater diversity of certain algal groups, such as the Chrysophyceae and desmids, but the overall influence on algal diversity is probably negative. Influences in the Arctic zone are lower than in the central zone but settlements and acidification are not unusual. In the Mediterranean zone there are few deep lakes that are not man-made by damming rivers.

Deep lakes, while more buffered from climate warming by sheer volume of water than shallow lakes, are already showing effects of climate change on regimes of mixing and thermal stratification. Ice forms later in winter and melts earlier in spring. They have responded to warmer winter and early spring temperatures by shallower mixing during winter and earlier spring thermal stratification, and increased density and biomass of plankton. Zooplankton growth, however, also occurs earlier and there may be earlier suppression of phytoplankton by zooplankton grazing (Straile, 2000; Anneville et al., 2005). Earlier warming and higher average water temperature often lead to deeper and longer-lasting stratification. This results in a longer-lasting dark hypolimnion, in which zooplankton prey may be able to find a refuge from visual predation by fish (Manca et al., 2007), but which is detrimental to some fish species that require cool, well-oxygenated water in summer. This may eliminate the summer refuges of coregonid fish that are cold-water adapted and more common in the Arctic region, but are important glacial relict fish in north-central Europe; they may become confined to the Arctic. Many invertebrate species in this region are probably highly cold-adapted and will become extinct but may be replaced through rapid evolutionary mechanisms by similar forms. Birds may bring in new plants and invertebrates, for many migrants move through the entire latitude of Europe.

Fish are major reflectants of climate change but in deep lakes perhaps have a less potent, though still measurable, effect on food webs than in shallow lakes. With a lesser risk of fish kills on hot summer nights than in shallow lakes, when oxygen concentrations may fall greatly, the deeper lakes may prove more resilient. Where lakes contain a mixture of warmer-adapted cyprinid fish and cold-adapted esocids, salmonids and coregonids, we expect a spread of cyprinids throughout the lake and this may have major consequences for commercial and recreational fisheries that usually favour the former groups. Mediterranean deep lakes will suffer lower water levels, raised salinities (Green et al., 1996) and elimination of much of their littoral zone with a major reduction in biodiversity. Their hypolimnia will deoxygenate but only to a slightly greater degree, for they already become seriously deoxygenated in summer.

The secondary effects of climate change may be serious because upland regions that presently do not support crop agriculture may be increasingly brought into cultivation, with increased nutrient run-off. Likewise, the colder uplands will be more favoured for settlement, leading to expansion of lakeside towns and greater effluent problems. Conversely, increased costs of oil (for reasons other than climate change) and attempts at limiting vehicle usage (because of carbon dioxide release) may lead to lowered NOx emissions and hence some reduction in nitrogen loading on upland lakes. This could well be completely offset, however, by changes in land use and settlement.

Conclusions

We approach future climate change from a baseline of freshwater habitats that are already seriously damaged, with the damage being greatest in the central and Mediterranean zones, but not insignificant in the extreme north. Only for very large, deep lakes do we have more than a handful of sites in central and southern Europe that can remotely approximate to pristine conditions. Six thousand years of progressive cultivation and settlement have rendered the concept of 'High ecological status' defined by the Water Framework Directive a largely hypothetical one, though the definition is being corrupted by official bodies (Moss, 2008). In assessing the effects of warming and associated changed hydrology, we thus start from a basis where many interacting factors have already reduced biodiversity and continue to threaten it.

We approach changes in biodiversity in the

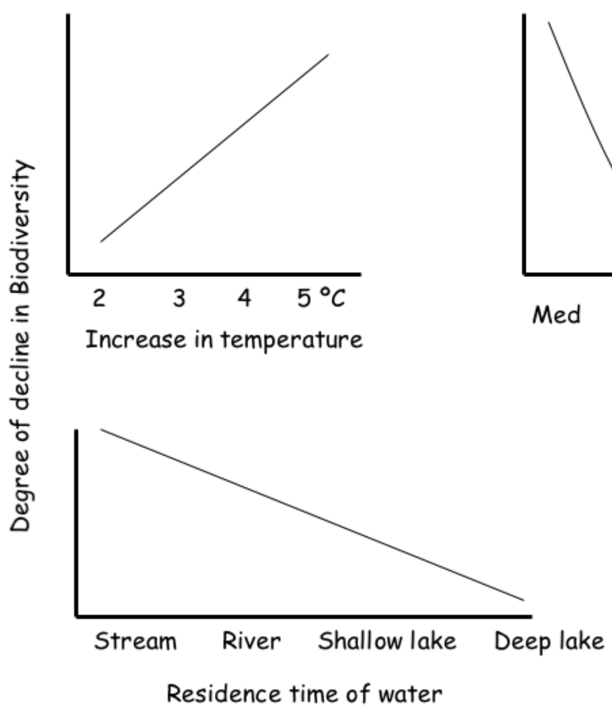

Fig. 5. Notional influences on rate of decline of biodiversity (in a wide sense) given increases in temperature, European latitude (taking into account the possibilities of invasion from the south) and residence time. The higher the temperature increase, the greater likelihood of decline due to lack of time for adjustment to occur. Invasion of the Mediterranean region from the south is hindered by marine barriers and although invasion of the Boreal/Arctic is possible, it will be counteracted by extinction of cold-adapted species. Long residence time gives a degree of resistance because it implies a larger system.

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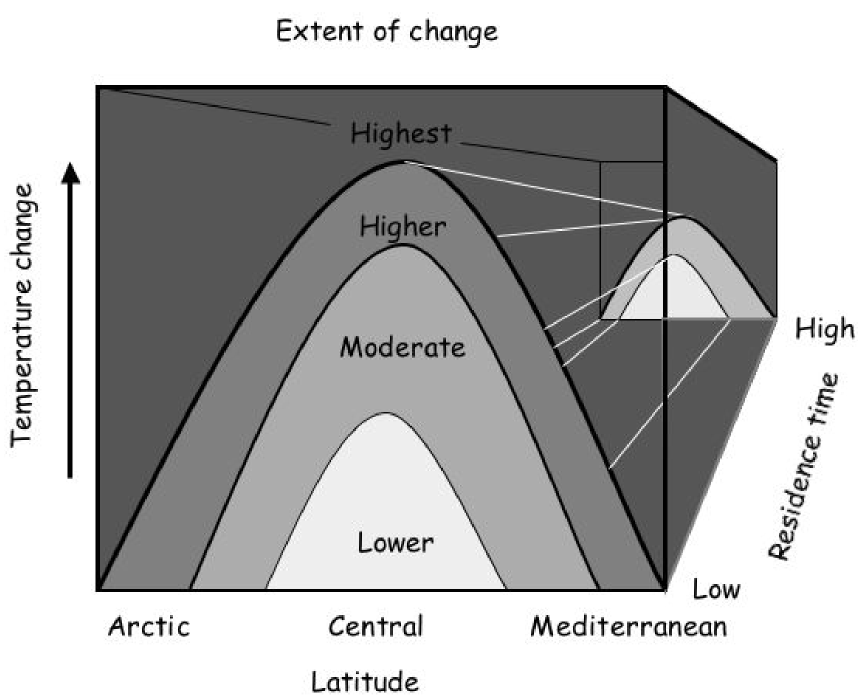

Fig. 6. Summarised combined effects of temperature increase with residence time of the water body and geographical location in Europe on degree of decline of biodiversity (in a wide sense). Position within the three-dimensional box indicates the degree of change in biodiversity from highest to lowest with denser shading indicating greatest change.

knowledge that with tens of thousands of species occurring in potentially trillions of combinations, with elements of randomness as well as determinism both by physico-chemical and biological mechanisms, and with continuous evolutionary change possible in every species, we have no hope of making sensible predictions beyond those that are very general. When human intervention is also programmed into this, even the generalities become very uncertain. It is like juggling with a trillion balls. The task is impossible. All that we can be certain of is that almost all of our habitats are severely damaged already and that warming is likely to worsen their quality in many ways. Fig. 5 summarises the likely degrees of change in biodiversity to be expected for the three broad European zones we have considered, in terms of increased temperature (and associated alterations in hydrology) and retention time of the water mass, as we move from upland erosive streams to floodplain rivers, shallow lakes and deep lakes. Fig. 6 combines these three variables into a picture that suggests that the major changes will be in the extreme north and in the south, that they will be greater the more marked the climate change, and that they will impact river systems most and deep lakes least. Finally, Tables 1, 2 & 3 summarise current major human impacts, additional impacts of warming and appropriate mitigation measures for maintenance of biodiversity in freshwater ecosystems.

There is increasing experimental evidence that the degree of pristine biodiversity has meaning and that we must view any substantial loss of it as serious. The operation of the engines of ecosystems is a function of availability of an appropriate range of components (Tilman et al., 1996; Hooper et al., 2005), with much built-in substitution (spare parts) to cope with naturally fluctuating conditions. If the emerging understanding of earth-systems-science states that our existence on this planet depends on the continued functioning of natural systems that regulate atmospheric and oceanic composition, we must be very concerned that these systems are being damaged so extensively. There are political hopes that climate change can be mitigated or adapted to, and some benefits will accrue from these. Our fears as professional ecologists, however, are that political institutions have isolated themselves so much from knowledge of the fundamental driving engines of the biosphere that they leave us with an increasingly defunct vehicle. Yet there remain skilled mechanics in the professional ecological community able to give better advice than those to whom policy-makers currently turn.

Table 1. Summary of current major human impacts, additional impacts of warming and appropriate mitigation measures, where possible, for maintenance of biodiversity in Boreal-Arctic freshwater ecosystems. The lists are not comprehensive.

	Present major impacts	Effects of warming	Mitigation
Boreal-Arctic erosive rivers	Relatively small in the Arctic; most Boreal rivers are dammed and catchments disrupted by forestry with toxic pollution (paper industry), eutrophication and acidification. Mobilisation of mercury in peaty areas.	Increased flow with glacier melt; loss of cold-water fish (especially salmonids and coregonids) and other animals; increased likelihood of damming for power generation.	Maintenance of intact forested corridors in the Boreal and continuation of measures to combat acidification. Problems need largely to be tackled at source (i.e. severe restriction of greenhouse gas emissions).
Boreal-Arctic depositional floodplain rivers	As for erosive rivers in this zone.	Changed pattern of flows with glacier melt and faster spring melt. Disruption of migratory fish runs. Loss of permafrost and greater coalescence of associated wetlands. Loss of cold-water animals and fisheries.	Maintenance of intact forested corridors in the Boreal, greater nutrient restriction and continued measures to combat acidification. Problems need to be tackled at source (i.e. severe restriction of greenhouse gas emissions).
Boreal-Arctic shallow lakes	As for erosive rivers in this zone.	Increased growth season for plants. Reduced season of ice cover and reduced winter deoxygenation. Greater nutrient input. Possible colonisation by fish of previously fishless lakes. Loss of cold-water fish. Invasion by exotic species. Increased release of carbon dioxide and methane from sediments and peats.	Greater nutrient restriction and continued measures to combat acidification. The system is too extensive for much individual mitigation. Problems need to be tackled at source (i.e. severe restriction of greenhouse gas emissions).
Boreal-Arctic deep lakes	As for erosive rivers in this zone.	Increased growth season. Greater hypolimnial deoxygenation. Greater nutrient input. Mismatches between algal, zooplankton and fish growth and changed fisheries. Loss of cold-water fish. Invasion by exotic species.	Greater nutrient restriction and continued measures to combat acidification. Local control of undesirable exotics may be possible. Problems need to be tackled at source (i.e. severe restriction of greenhouse gas emissions).

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Table 2. Summary of current major human impacts, additional impacts of warming and appropriate mitigation measures, where possible, for maintenance of biodiversity in Central-European freshwater ecosystems. The lists are not comprehensive.

	Present major impacts	Effects of warming	Mitigation
Central erosive rivers	Already very severe modification. Acidification, damming, eutrophication from atmospheric nitrogen sources and upland farming, and deforestation of catchment. Afforestation of catchment with exotic softwoods disrupts food sources. Channel engineering.	General change in temperature, flows and seasonality will exacerbate most existing problems. Farming at higher elevations will exacerbate eutrophication. Replacement of cool water species by warmer water species. More damming for power generation, and for water storage for irrigation and domestic supply. Some invasion of exotic species.	Afforestation of wide river corridors with native trees. Nutrient management on farms. Restrictions on fuel consumption and land fertilisation may alleviate nitrogen acidification. Reservoir management must incorporate more sensitive flow and water level control to protect downstream systems.
Central depositional floodplain rivers	Already devastated by engineering works involving drainage and channelisation. Few floodplains remain intact.	More summer deoxygenation in engineered channels and fish kills. Greater symptoms of eutrophication. Loss of many fish species. Invasion of exotics likely to be severe.	Restoration of floodplain progressively from upstream to downstream. Nutrient management. Full enactment of Water Framework Directive to restore systems to good ecological quality.
Central shallow lakes	Severe eutrophication. Introduction of damaging fish (e.g. common carp). Recreational damage by boats. Run-off of agricultural biocides.	Increased symptoms of eutrophication. Increased deoxygenation, greater but less diverse plant growth, risk of summer fish kills, especially of piscivores. Increased release of carbon dioxide and methane from sediments. Higher dominance of small cyprinid fish. Invasion by undesirable exotics. Increased nutrient loading from more intensive farming for food and biofuels. Water level reduction from increased irrigation in general area. Flooding by sea in coastal areas as sea levels rise and complete loss of some lagoonal systems.	Extensive nutrient management. Fisheries management to exclude undesirable invaders and maintain balanced community with piscivores. Irrigation restrictions to maintain water supply. Intensive nutrient management for agriculture and urban sources. Restoration of construction of surrounding wetlands. Probably too expensive to protect coastal lagoonal systems from sea-level rise.
Central deep lakes	Acidification in uplands, eutrophication almost everywhere. Engineering to raise and control levels for water supply and loss of littoral zones	As for Boreal-Arctic deep lakes but with markedly increased symptoms of eutrophication; greater hypolimnial deoxygenation and almost complete loss of salmonid and coregonid fish. Greater dominance of small cyprinid fish. More intervention to control water levels.	Intensive nutrient management. Fisheries management to exclude invaders and maintain balanced community with piscivores. Restriction of vehicle usage to minimise nitrogen acidification and eutrophication problems. Full enactment of provisions of Water Framework Directive.

Table 3. Summary of current major human impacts, additional impacts of warming and appropriate mitigation measures, where possible, for maintenance of biodiversity in Mediterranean freshwater ecosystems. The lists are not comprehensive.

	Present major impacts	Effects of warming	Mitigation
Mediterranean erosive rivers	Eutrophication, exacerbated by upland forest fires. Loss of forested riparian corridors to farming. Damming for water storage and inadequate compensation flows. Some exotic species causing severe problems, especially fish and crayfish.	Severe effects with reduction in summer flows. Many may become completely dry with loss of biodiversity. Severe deoxygenation and increased salinity in those that persist with major loss of fish and invertebrates. More invasion of exotic species.	Increased compensation flow from water storage reservoirs. Re-establishment of forest corridors and rigorous control of non-natural fires. Abandonment of agriculture in arid areas. Problems need to be tackled at source (i.e. severe restriction of greenhouse gas emissions).
Mediterranean depositional floodplain rivers	Already devastated by engineering works involving drainage and channelisation. No floodplains remain intact.	More summer deoxygenation in engineered channels and fish kills. Greater symptoms of eutrophication. Greater salinification. Loss of many fish species. Invasion of exotics likely to be severe.	Restriction of irrigated agriculture in arid areas. Removal of dams. Restoration of floodplain progressively from upstream to downstream. Nutrient management. Full enaction of Water Framework Directive to restore systems to good ecological quality.
Mediterranean shallow lakes	Increased salinity owing to loss of natural water supply to irrigation. Complete drying out in many cases. Eutrophication from farming.	More will completely dry out in summer, becoming intensely saline as they do so with restriction, then loss of the biota. Major loss of endemic fish and amphibian species. Eutrophication symptoms will increase (particularly cyanobacterial blooms) in those that persist.	Nutrient management and greater restriction on use of water for irrigation will help, as will full enaction of Water Framework Directive to restore systems to good ecological quality. Problems need to be tackled at source (i.e. severe restriction of greenhouse gas emissions).
Mediterranean deep lakes	There are few of these and most are artificial reservoirs, suffering from extreme fluctuation in water level and severe eutrophication, except in the uplands.	Intensification of existing problems, particularly loss of littoral zones and fish spawning habitat owing to extreme drawdown. More intense and frequent algal blooms as temperatures rise.	Better nutrient management, and severe restrictions on irrigation and urban development. Problems need to be tackled at source (i.e. severe restriction of greenhouse gas emissions).

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Author Profile

Brian Moss: Fresh waters have always been a major part of Brian's life, since learning about the dramatic story of how lakes stratify in his undergraduate career nearly half a century ago, and the stimulation of visiting, as a postgraduate, the enormously friendly FBA laboratory on Windermere. Thereafter he has carried out freshwater research in Africa, the United States and Europe and has taught freshwater science on almost all the continents. The work has involved many approaches, from field observations to experiments in the lab, in mesocosms, experimental tanks and whole lakes and has centred on eutrophication, lake restoration and the effects of climate change. He is presently Holbrook Gaskell Professor of Botany at the University of Liverpool, UK and President of the International Society for Limnology. When he is not happily getting wet and muddy, he plays the double bass and writes poems.

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