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GLOBIO-Aquatic, a global model of human impact on the biodiversity of inland aquatic ecosystems

J.H. Janse[a,b,*], J.J. Kuiper[a,b], M.J. Weijters[c,1], E.P. Westerbeek[a,2], M.H.J.L. Jeuken[a,3], M. Bakkenes[a], R. Alkemade[a,d], W.M. Mooij[b,e], J.T.A. Verhoeven[c]

[a] PBL, Netherlands Environmental Assessment Agency, Dept. of Nature and Rural Areas, P.O. Box 303, NL-3720 AH Bilthoven, The Netherlands
[b] Netherlands Institute of Ecology (NIOO-KNAW), Dept. of Aquatic Ecology, P.O. Box 50, NL-6700 AB Wageningen, The Netherlands
[c] Ecology and Biodiversity, Institute of Environmental Biology, Utrecht University, Padualaan 8, NL-3584 CH Utrecht, The Netherlands
[d] Wageningen University, Environmental Systems Analysis, P.O. Box 47, NL-6700 AA Wageningen, The Netherlands
[e] Wageningen University, Aquatic Ecology and Water Management, P.O. Box 47, NL-6700 AA Wageningen, The Netherlands

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ABSTRACT

Biodiversity in freshwater ecosystems – rivers, lakes and wetlands – is undergoing rapid global decline. Major drivers are land use change, eutrophication, hydrological disturbance, climate change, overexploitation and invasive species. We developed a global model for assessing the dominant human impacts on inland aquatic biodiversity. The system consists of a biodiversity model, named GLOBIO-Aquatic, that is embedded in the IMAGE model framework, i.e. linked to models for demography, economy, land use changes, climate change, nutrient emissions, a global hydrological model and a global map of water bodies. The biodiversity model is based on a recompilation of existing data, thereby scaling-up from local/regional case-studies to global trends. We compared species composition in impacted lakes, rivers and wetlands to that in comparable undisturbed systems. We focussed on broad categories of human-induced pressures that are relevant at the global scale. The drivers currently included are catchment land use changes and nutrient loading affecting water quality, and hydrological disturbance and climate change affecting water quantity. The resulting relative mean abundance of original species is used as indicator for biodiversity intactness. For lakes, we used dominance of harmful algal blooms as an additional indicator. The results show that there is a significant negative relation between biodiversity intactness and these stressors in all types of freshwater ecosystems. In heavily used catchments, standing water bodies would lose about 80% of their biodiversity intactness and running waters about 70%, while severe hydrological disturbance would result in losses

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[*] *Corresponding author at*: PBL, Netherlands Environmental Assessment Agency, Dept. of Nature and Rural Areas, P.O. Box 303, NL-3720 AH Bilthoven, The Netherlands. Tel.: +31 6 50834609.
E-mail address: jan.janse@pbl.nl (J.H. Janse).
[1] Present address: B-ware, Nijmegen, The Netherlands.
[2] Present address: Mangrove Info & Kayak Centre, Bonaire, Caribbean, The Netherlands.
[3] Present address: Deltares, Delft, The Netherlands.

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of about 80% in running waters and more than 50% in floodplain wetlands. As an illustration, an analysis using the OECD 'baseline scenario' shows a considerable decline of the biodiversity intactness in *still existing* water bodies in 2000, especially in temperate and subtropical regions, and a further decline especially in tropical regions in 2050. Historical loss of wetland areas is not yet included in these results. The model may inform policy makers at the global level in what regions aquatic biodiversity will be affected most and by what causes, and allows for scenario analysis to evaluate policy options.

1. Introduction

An estimated 11–13 million km^2, or 8–9% of the earth's continental surface consists of inland aquatic ecosystems, of which about 21% are lakes, 3% reservoirs, 3% rivers, 33% floodplain marshes and swamps, 6% coastal wetlands, and 35% other wetlands (Lehner and Döll, 2004). These systems host a high and unique biodiversity and deliver important ecosystem services like freshwater availability, water purification, climate regulation, food and recreational values (MEA, 2005a).

Global freshwater biodiversity is declining and is expected to further decline (MEA, 2005b; Revenga et al., 2005; CBD, 2014), possibly at even higher rates than in terrestrial and marine habitats (Loh and Wackernagel, 2012). Aquatic systems are especially vulnerable because human population density is on average higher near lakes, rivers and estuaries, and because water bodies accumulate the effects of developments in their catchment (Williamson et al., 2008). Population increase, economic development, food and fuel demand and urbanization are the main *indirect* anthropogenic drivers causing this decline of biodiversity at the global scale. These lead to manifold *direct* drivers of change which can be assigned to several broad categories: land-use changes, hydrological disturbance (both leading to loss of habitats), pollution, climate change, overexploitation and exotic species are the most-mentioned ones (Sala et al., 2000; Revenga et al., 2005; MEA, 2005b; Dudgeon et al., 2006).

One of the most prominent direct drivers contributing to the decline of aquatic biodiversity at a global scale is land use change, which involves both the direct conversion of wetlands as well as indirect effects of land-use in the catchment (Watzin and McIntosh, 1999; Allan, 2004; Revenga et al., 2005; Verhoeven et al., 2006). Recent estimates state that over 60% of wetland area has been converted worldwide since 1900 (Davidson, 2014). Indirect effects of land-use changes include elevated suspended solid concentrations resulting from increased erosion after deforestation (Wissmar et al., 2004; Cohen et al., 1993), eutrophication (nutrient concentrations generally strongly correlate with the intensity of land use in the upstream catchment (Crosbie and Chow-Fraser, 1999; Harper, 1992)), and increased pollution by other (toxic) substances. A combination of these and other factors related to land-use changes leads to changes in river channels and floodplains that disturb the natural habitats of aquatic biota (Allan, 2004).

A second important category contributing to a global decline in aquatic biodiversity is hydrological disturbance resulting from water withdrawal for e.g. irrigation and public water supply, and from regulation of water flows by infrastructure for e.g. hydropower generation, protection against flooding, navigation or water storage (Rosenberg et al., 2000; Bunn and Arthington, 2002). By 2010 there were about 50,000 dams (higher than 15 m), creating a total area of about 300,000 km^2 of reservoirs and impacting some 70% of the world's rivers (Lehner et al., 2011). Dams affect biota via disruption of the natural flow regime or the seasonal flood pulse to which organisms are adapted (Ward, 1998; Keddy et al., 2009) and by blocking migration routes (Poff et al., 1997; Poff and Zimmerman, 2010). In wetlands and lakes, hydrological alternation may cause changes in water level, flooding or desiccation (Nilsson and Berggren, 2000; Wantzen et al., 2008).

Recently global climate change has been identified as a dominant driver of change affecting aquatic ecosystems in several ways (e.g. Palmer et al., 2008; Mooij et al., 2005; Moss et al., 2009; Vescovi et al., 2009), including rise in water temperature and hydrological changes (such as increased peak discharges or long periods of low flow). The latter may also lead to increased nutrient loading and, in some regions, salinization. In streams, temperature increase may lead to extinction of characteristic species. In standing waters, biotic communities will be affected by a range of processes, like increased frequency of stratification periods, productivity increases and algal blooms. Climate change can aggravate the effects of eutrophication (Mooij et al., 2005; Jeppesen et al., 2009; Moss et al., 2011).

Many other factors have been described as influencing biodiversity at various scales, such as invasions of exotic species (e.g. Sala et al., 2000; Leprieur et al., 2009) and the exploitation of aquatic biota (FAO, 2012) including the harvest of food (fish, crustaceans and other organisms) and fibre (reed, papyrus). In addition, water bodies are increasingly used for aquaculture, a booming sector, which is already responsible for about half of the world's fish production for human consumption, of which 80% takes place in freshwaters, mainly in Asia (FAO, 2012). Impacts include eutrophication, pollution, escape of cultured organisms to the wild and spread of diseases. Additional factors influencing biodiversity at various scales are local habitat changes, acidification, salinization, organic pollution, genetic disruption and toxic stress.

The worldwide losses of biodiversity and ecosystem services are a major concern to policy makers at the local, national and international level. Examples of the latter are international forums like the Convention on Biological Diversity (CBD), Ramsar Convention on Wetlands, EU, OECD and other agencies, international NGO's and companies. To evaluate policy options, there is a great need for integrated models that dynamically describe the drivers of change and their impact on biodiversity (MEA, 2005b; Pereira and Cooper, 2006; Dudgeon, 2010; CBD, 2014).

Several global models exist that describe important drivers of change, such as climate, hydrology (Vörösmarty et al., 2000; Döll et al., 2009; Biemans et al., 2011; Van Beek et al., 2011) and nutrient loading (Seitzinger et al., 2010; Bouwman et al., 2011). Vörösmarty et al. (2010) made an integrated model of threats to biodiversity in rivers. Most generic simulation models on ecological processes (see for instance overview for lakes by Mooij et al. (2010)) do not specifically address biodiversity, although correlative models have been developed for species composition related to abiotic factors (see e.g. overview for streams by Verdonschot (2000)). These models, however, are generally confined to smaller spatial scales or specific water types. Direct correlation between species distribution data and abiotic data at larger scales have produced much insight, but may fail to discern natural and anthropogenic factors or may give misleading results due to covariation between factors (e.g. Xenopoulos et al., 2005). In conclusion, a broad, overarching and consistent model of the human impacts on aquatic biodiversity in inland waters is not yet available. This paper describes the outlines of such a global model, called GLOBIO-Aquatic.

GLOBIO-Aquatic models the dominant human impacts on inland aquatic biodiversity using a meta-analysis of existing information. It consists of a set of empirical relationships between environmental drivers and their impact on biodiversity in different aquatic ecosystems. The focus is on broad categories of human-induced pressures that still hold when scaled up from a local/regional level to the global level. Currently the drivers *land-use change* (including eutrophication), *hydrological disturbance* and *climate change* are investigated. The severity of impacts is expressed as a biotic intactness index relative to the respective reference composition (i.e. in the undisturbed state; see Section 2.2). This allows studying the impacts of different drivers in concert, and comparing their impacts among different types of aquatic ecosystems. Hence, we do not aim to 'explain' the biodiversity patterns in all kinds of aquatic ecosystems, but rather to 'extract' the impact of the main anthropogenic pressures on the natural species pattern. The model is embedded in the IMAGE model framework for land use and global environmental change (Stehfest et al., 2014) and is complementary to the GLOBIO model for terrestrial ecosystems (Alkemade et al., 2009).

We first describe the chain of models to estimate the magnitude of the main drivers of change. We then present the biodiversity intactness indicators. We document how we linked the above-mentioned drivers and the biodiversity of rivers, lakes and wetlands and compare the biodiversity impact among different ecosystems. Finally, we present the implementation and application of the model chain, and use a global baseline scenario (OECD, 2012) for the period 2000–2050 as an example.

2. Methods

2.1. Drivers and model chain

The environmental drivers are evaluated through a chain of global models and maps consisting of a land use and climate change model, a hydrological model, a nutrient model and a map of the water bodies. The catchment approach is applied by including the spatial relations between pixels, based on flow direction. Fig. 1 shows schematically the relationships between the models for the drivers currently addressed.

Projections of land use and climate change are derived from the IMAGE model (Stehfest et al., 2014) that uses projections on human population size, economic growth, food and energy requirements, and food trade, to model future agricultural land use. Based on the requirements and sources of energy, IMAGE also models the world's carbon emissions and climatic changes such as temperature, precipitation and potential evapotranspiration. The Global Nutrient Model (Beusen, 2014) translates future population size and agricultural land-use patterns into soil nutrient budgets (Bouwman et al., 2011) and nutrient loadings to aquatic systems, from both diffuse and point sources. Nitrogen and phosphorus leaching and runoff from the land to the surface waters is modelled based on agricultural area, the application of fertilizer and manure, precipitation and spatial characteristics of slope, soil texture and groundwater characteristics. Urban nutrient emissions are modelled based on population, affluence (GDP), sanitation and the use of detergents (Van Drecht et al., 2009). Retention of nutrients in the global surface water network is included, based on slope and retention time.

Water discharge is calculated by the global hydrological model PCR-GLOBWB (Van Beek and Bierkens, 2009) or the hydrological module of the global vegetation model LPJmL (Biemans et al., 2011). The discharge is based on a water balance per pixel, including precipitation, evapotranspiration, snowmelt, infiltration to groundwater and human water abstraction. In these models, the discharge is affected by climatic variables, land use, water abstraction, and by the presence and way of management of dams and reservoirs. The two models differ in time scale, in the schematization of river floodplains and wetlands and in the definition of vegetation and crop types. The model PCR-GLOBWB also calculates the water temperature (which is currently used for the algal bloom indicator only; see Section 2.5). Data on existing dams are taken from the GRAND database (Lehner et al., 2011) and a projection of future dams made according to Fekete et al. (2010).

The deviation between natural and impacted flow pattern is derived from the modelled discharges as the 'amended annual proportional flow deviation' (AAPFD; Ladson and White, 1999 and implemented as described by Biemans et al., 2011):

$$\mathrm{AAPFD} = \left[\sum_{i=1}^{12}\left(\frac{Q_i - Q_{i0}}{\bar{Q}_{i0}}\right)^2\right]^{\frac{1}{2}} \tag{1}$$

This deviation is averaged over the years of record. In the formula, Q_i stands for the runoff in the ith month, Q_{i0} for the

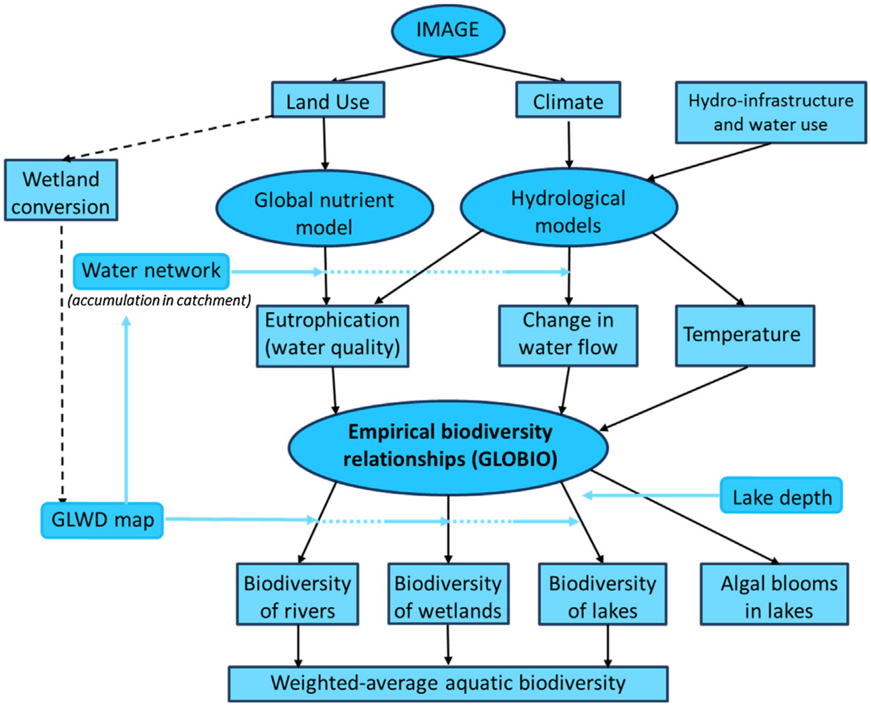


Fig. 1 – Model chain for freshwater biodiversity. Rectangles denote variables or processes, ovals denote models, rounded rectangles denote data, black arrows denote model input or output, blue arrows (in web version) or grey arrows (in print version) denote data input.

natural runoff in the ith month and $\bar{Q}_{i0}$ for the year-averaged natural runoff. The value of AAPFD may range from 0 for unregulated rivers to $+\infty$; in general, values above 3 denote a strong deviation.

Drivers are currently modelled in a spatial resolution of $30' \times 30'$ (approx. 50 km × 50 km at the equator). All fluxes are accumulated downstream according to the water routing routine, which is based on a digital elevation map (DEM). The location and type of water bodies is based on the Global Lakes and Wetlands Database map (Lehner and Döll, 2004), which is available at different resolutions. This map discerns the main inland water types: lakes, reservoirs, rivers and several types of wetlands namely riverine marshes and swamps, isolated wetlands (bogs, etc.), intermediate, brackish and coastal wetlands as well as wetland mosaics. From the GLWD we calculated the fractional area of each type of surface water in each grid cell. The routing model and GLWD map are combined to estimate the nutrient loadings to the water bodies of the GLWD categories 1–6 (i.e. lakes, reservoirs, rivers, floodplain wetlands, swamps and coastal wetlands) and the fraction of human land use in their upstream catchment. The other wetland types (categories 7–12) are assumed to be more isolated and hence to have their catchments confined to only the grid cell in which they are located. Data on lake depths are (if available) derived from the ‘FLAKE’ dataset (Kourzeneva, 2010). Lakes are divided into the categories ‘shallow’ and ‘deep’ based on a boundary value of 3 m mean depth. In case of multiple values within a cell, a frequency distribution of these categories is calculated. Missing values are estimated by (in this order): (a) the elevation map: lakes in mountainous regions are assumed to be deep; (b) expert judgement based on regional characteristics; (c) nearest neighbour (only within a biome); and (d) the world average (per category).

All aforementioned drivers are confined to the existing water bodies (i.e. defined in the GLWD-2004, based on data from the 1990s). As there are no historical lake and wetland maps available to estimate historical wetland conversions, a first attempt was made to derive such a map from model calculations (Brolsma et al., 2012). The model PCR-GLOBWB (Van Beek et al., 2011; Van Beek and Bierkens, 2009) was run with only natural hydrological input, excluding all human interventions, and all permanently inundated areas were selected. This gives an estimate of all potential natural wetlands (disregarding historical climate change). For future projections of wetland conversion to human land use, a model was made by Van Asselen et al. (2013) based on a meta-analysis of conversions that have occurred in the last century. The conversion risk can be calculated from a number of physical and socio-economic drivers, of which agricultural demand appeared to be prominent. But this study did not cover the factors determining the precedence of wetlands or other land cover types for conversion. As these modules are still in development, they have not yet been included in the version documented in this paper. Instead, as a conservative guess, a minimum estimate of wetland conversion was made, based on the area of GLWD wetlands minimally required to meet the projected increase in agricultural land demand if all non-wetland areas (such as forests) have been used.

2.2. *Biodiversity indicators*

To express biodiversity, we used indicators that allowed us to quantify and compare the ecological impact for highly different studies and ecosystem types. The most important indicator used in this study is 'biodiversity intactness' or 'naturalness' of the biotic community, denoted as 'MSA' (Mean relative Abundance of original Species) (Alkemade et al., 2009). This indicator, also referred to as 'relative taxon richness (RTR)' (Verboom et al., 2007; Weijters et al., 2009), is related to the Biological Intactness Index (BII) (Scholes and Biggs, 2005) and is also used in the terrestrial GLOBIO model. The MSA calculates as the average remaining abundance of originally occurring species, relative to the corresponding natural abundance, on a 0–1 scale:

$$\mathrm{MSA}_s = \frac{\sum_i R_{is}}{N} \tag{2a}$$

$$R_{is} = \frac{A_{isd}}{A_{isc}} \tag{2b}$$

where MSA_s is the mean relative abundance of the original species estimated in study *s*, *N* the number of species in the study, and R_{is} the ratio between the abundance of species *i* in the disturbed (A_{isd}) and the corresponding undisturbed (reference) situation (A_{isc}), respectively. The 'reference situation' may be the situation of the same water body before the disturbance occurred, or a naturally comparable undisturbed water body in the same region. The abundance of a species may be given as number of individuals per site, the number of sites at which the species is found, the pooled abundance over the year, or a comparable metric that fulfils the overall aim of a metric of the degree of occurrence of the species. Only those species that occur in the reference situation are included, and the ratio for each species is truncated at 1: an increase of a species beyond its 'undisturbed' density is not considered as an improvement. The MSA concept allows scaling and comparing different ecosystem types. It differs from species richness or other diversity indicators like the Shannon–Wiener index in that species that only occur in the disturbed and not in the undisturbed ('pristine') situation, are not included. Invasion by 'exotic' species is not reflected in the indicator, but is indirectly accounted for by an assumed link with a decline of native species.

The MSA indicator is related to the widely used Index of Biotic Integrity (IBI), a multi-metric index that describes an ecosystem's biotic community compared with its undisturbed state. The original version of the IBI (Karr, 1981), based on fish data, had 12 metrics with values between 1 (disturbed) and 5 (pristine), and hence cumulative ranges between 12 and 60. The IBI method has been further developed and (regionally) adapted for many different ecosystems and biotic groups (Karr and Chu, 2000; Wright et al., 2000; Parsons et al., 2002), with varying number and nature of metrics. For studies in which only the IBI values were reported instead of the raw data, we transferred these into MSA values by rescaling them between 0 and 1 for the minimum and maximum IBI values, respectively, assuming linear interpolation. So,

$$\mathrm{MSA} = \frac{\mathrm{IBI} - \mathrm{IBI}_{\mathrm{min}}}{\mathrm{IBI}_{\mathrm{max}} - \mathrm{IBI}_{\mathrm{min}}} \tag{3}$$

In studies where species presence or abundance data (allowing MSA calculation) were published besides IBI scores (e.g. Crewe and Timmermans, 2005), the correlation between the two was high ($r^2 = 0.62$), justifying the use of both indicators in this study.

The MSA can also be linked to the Ecological Quality Ratio (EQR) used in the European Water Framework Directive. This is also an indicator, scaled 0–1, based on the biota (species composition and abundance of functional groups) relative to the reference condition of the respective water type. The EQR uses data on macrophytes, algae, macro-invertebrates and fish. Although the EQR calculation process is complicated and not necessarily linear, in this study the EQR has been converted 1:1 into MSA for the cases concerned. In a scoping study in The Netherlands, the average values of both indicators were in good agreement (PBL, 2008), but a more rigorous comparison would be needed.

Complementary to the MSA, the occurrence of harmful algal blooms (primarily cyanobacteria) has been included as an indicator for the ecological status of lakes. Algal blooms are often used as a disturbance indicator, generally negatively related to MSA, as phytoplankton dominance excludes other native species. The algal bloom module is included to cover the impacts of climate change in terms of temperature rise.

2.3. *Data collection*

The relation between the selected environmental drivers and the biodiversity in rivers, lakes and wetlands, was based on meta-analyses of literature data. Studies were selected in which biodiversity data in impacted systems had been compared with those in undisturbed reference systems, either in time (before–after) or space (provided the systems were comparable concerning natural factors). Case studies were derived from literature published in scientific journals, reports or books, disclosed by online search engines (Scopus, Google Scholar and Web of Science) and/or referenced in review papers and, occasionally, on datasets obtained through personal communication. Grey literature has not been surveyed. Search terms were grouped in four categories, comprising the ecosystem type under concern, the driver of interest, the effect parameters, and the type of study (comparator), respectively (Table 1). Search terms were combined to select papers that contained at least one term from each group in their title, key words or abstract. From the hits, we selected papers that met the following criteria:

- The studies compared disturbed systems with reference systems (in time or space).
- The studies clearly defined the nature and the degree of the disturbance.
- The studies reported on species richness, species composition, Index of Biotic Integrity (IBI) or Ecological Quality Ratio (EQR).

These criteria were applied with some flexibility, in that the definitions of the reference state or the description of the degree of disturbance may sometimes differ among studies or required some translation (explained below) or, as pointed out, that sometimes derived data were used as a proxy for MSA if primary species data were not published.

Table 1 – Search terms for the literature surveys.

Theme #	Ecosystem	Drivers	Effect parameters	Comparator
1[1]	Stream River	Land use Land cover Catchment Watershed Urban land use Agricultural land use Anthropogenic disturbance Human impact Deforestation Eutrophication Phosphorus Nitrogen	Biodiversity Species composition Community Species richness Biotic integrity IBI Macro-invertebrates Fish Macrophytes Vegetation Phytoplankton Zooplankton Amphibia Reptiles Birds Mammals	Impact assessment Pristine Reference
2	Wetland	Idem as 1	Idem as 1	Idem as 1
3	Lake	Idem as 1	Idem as 1	Idem as 1
4	River Stream	River regulation/alteration Flow regulation/alteration Flow regime Altered hydrology Altered flooding Hydrologic(al) change/alteration/regime Flow disturbance Flood pulse/regime Inundation period/frequency	Idem as 1	Idem as 1
5[2]	Floodplain wetland Riverine wetland Riparian wetland	Idem as 4	Idem as 1	Idem as 1

[1] Weijters et al. (2009).

[2] Kuiper et al. (2014).

For land use changes in the catchment and eutrophication, we analyzed the effect on the biodiversity of (1) rivers and streams, (2) wetlands and (3) lakes. Accordingly, we analyzed the effect of hydrological disturbance on the biodiversity of (4) rivers and streams, and (5) floodplain wetlands. Table 1 shows the search terms used in the search query.

The effect of *land use changes* on *rivers and streams* (Weijters et al., 2009) was based on studies on biodiversity in rivers and streams with different catchment land use (forest, agricultural, urban, etc.) and/or different nutrient concentrations in the water. As water nutrient concentrations generally strongly correlate with land use in the upstream catchment (e.g. Harper, 1992; Johnes et al., 1996; Crosbie and Chow-Fraser, 1999) these variables might be used as interchangeable disturbance indicators. As land use gradients in river catchments often parallel natural gradients (Watzin and McIntosh, 1999; Allan, 2004), we only compared sites located in comparable river segments with similar stream order.

For the effects of *land use changes* on *wetlands* we based land use intensity on land use fractions, nutrient levels or disturbance rank, whatever reported. The results were categorized in the wetland classes defined in the GLWD (Lehner and Döll, 2004).

For *lakes*, the analysis was mainly based on phosphorus and nitrogen concentrations as an indicator for land use intensity in the catchment, partly for data reasons and also because eutrophication by nutrients is often the direct driver for effects on biodiversity in lakes.

We derived impacts of *hydrological disturbance* on *rivers* comparing data on biota in rivers at different degrees of regulation (mostly by dams, in some cases by canalization or water abstraction) to the situation before the impact, or to neighbouring unregulated river stretches. Not all studies reported the *degree* of flow disturbance in a uniform way. If reported, the AAPFD was used, in other cases an estimate was made.

In the study on *hydrological disturbance* on *floodplain wetlands* (Kuiper et al., 2014), the flow disturbance has been expressed in the categories low, medium or high. This study covers the GLWD wetland types 4 (floodplain marshes) and 5 (swamp forests).

2.4. *Data processing and combination*

Biodiversity intactness (MSA) values were calculated or estimated from the primary species composition data that were extracted from the case studies (Eq. (2)). IBI scores were translated into MSA according to Eq. (3) and EQR values were set equal to MSA. From each study, all available data points were used and depicted in the graphs (see Section 3).

For themes 1–4, a regression analysis between the disturbance variables and the MSA values was done, using the package *stats* version 3.2.0 available in R version 3.1.1 (R-Core-Team, 2014). In accordance with the definition of MSA, the regressions were forced to 1 at zero or minimum value of the disturbance factor. In themes 1 and 2 a linear relationship between disturbance level and MSA was assumed. In theme 3, logistic regressions have been performed, based on assumed non-linear (sigmoidal) relationships between nutrient concentrations and ecological effects (e.g. Scheffer et al., 1993). The regressions were done for shallow and deep lakes separately. In theme 4 we used the log 10 of the disturbance level, i.e. the AAPFD, as this variable varies between 0 and $+\infty$. In theme 5 data points were grouped into three levels of disturbance. We used meta-analyses to calculate mean effect sizes using the package *metafor* in R (for details see Kuiper et al., 2014). The data sets did not allow to calculate possible interactions between the different categories of drivers, which were therefore not included.

2.5. *Algal bloom module*

The algal bloom module calculates the probability of the dominance of harmful algal blooms of cyanobacteria in lakes. Several empirical models already exist that relate cyanobacterial biomass to total phosphorus (TP) and total nitrogen (TN) concentrations and water temperature, developed by Smith (1985), Watson et al. (1997), Downing et al. (2001), Håkanson et al. (2007) and Kosten et al. (2012). The model by Håkanson et al. (2007) (see Table 2) (slightly modified by adding a cut-off at TP below 0.005 mg L^{-1}) was used in this study, as it was judged as the most comprehensive and easy-to-use on a global scale.

2.6. *Implementation and application*

The model chain has been implemented, parallel to the GLOBIO-Terrestrial model, in Delphi in the software package Arisflow to control a correct handling of input data and calculations. Spatial data on land-use, water discharge, nutrient concentrations and flow deviation (calculated as explained in Section 2.1) were read from GIS files and combined with the regressions from the meta-analyses, applied for the water types present in each $30' \times 30'$ pixel according to the GLWD map. As the impacts of the different drivers are assumed to be independent, the MSA value per water body has been obtained by multiplying the values for the relevant drivers. The final indicator 'aquatic MSA' per pixel has been calculated by area-weighted averaging of the MSA values for rivers, lakes and wetlands as far as they occur in the particular pixel.

To illustrate its applicability at the global level, the model chain including GLOBIO-Aquatic has been applied for the 2000 situation and for 2050 according to the OECD baseline scenario (OECD, 2012). The main differences between those years are a 40% global population increase (from 6.5 to 9 billion people), a 60% increase of food production and energy demand (with 80% fossil fuel), a 4 degrees increase of average air temperature, a 50% increase in hydropower capacity, a 55% higher freshwater use and an increase in urban (doubling) and diffuse (20–50% higher) nutrient emissions to water.

3. Results

3.1. *Biodiversity relations*

3.1.1. *Land use changes*

Rivers and streams: The literature search gave about 240 papers, from which only 12 papers presented data applicable for a quantitative analysis of MSA, resulting in 18 relationships (Weijters et al., 2009). The most commonly reported groups were macro-invertebrates and fishes and all data were based on spatial comparison of sites. In the majority of the cases, total taxon richness decreased with increasing human land-use (urban or agricultural) in the catchment and with increasing nutrient concentrations (Fig. 2, Table 2), but there were also quite some opposite or indifferent examples and the variability between the studies was large (Fig. 2). Subgroup analysis revealed that fish tend to be more sensitive than macroinvertebrates (for details see Weijters et al., 2009).

Wetlands: The search resulted in nearly 400 articles, of which 35 reported on qualitative relations with species richness, but only 12 papers with quantitative data for MSA calculation (24 relationships). All studies involved spatial comparisons or gradient studies. A variety of biotic groups was represented in the dataset: plants, mosses, fishes, amphibians, macro-invertebrates, birds, mammals. The GWLD classes 4 (floodplain marshes), 5 (swamp forests), 6 (coastal wetlands) and 9 (intermittent or isolated wetlands) are the wetland types included. The classes 7 (brackish wetlands) and 8 (bogs, fens and mires) were underrepresented in the dataset. Our literature study reveals that species richness in wetlands is always negatively related to human land use in the catchment (Fig. 3, Table 2) and in most cases positively related to forest cover (data not shown). The data set was too small for conclusions on subsets or cofactors.

Lakes: In this survey 17 papers were found from which MSA values could be derived, mostly from comparisons between lakes, some from time series, and some from already compiled

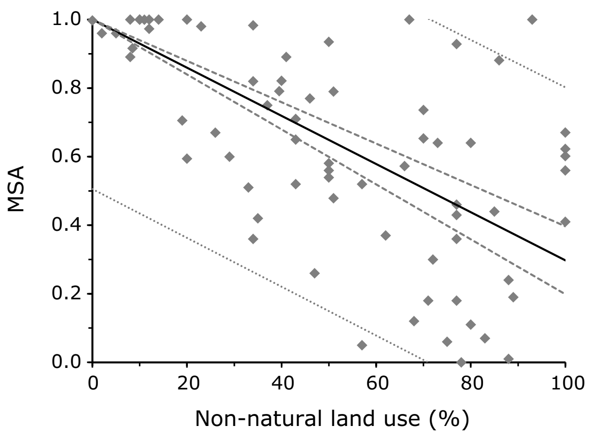


Fig. 2 – MSA in rivers and streams in relation to land use in the catchment (adapted from Weijters et al., 2009), including the regression line (black line; $R^2 = 0.33$), confidence interval (grey dashed line) and prediction interval (grey dotted line).

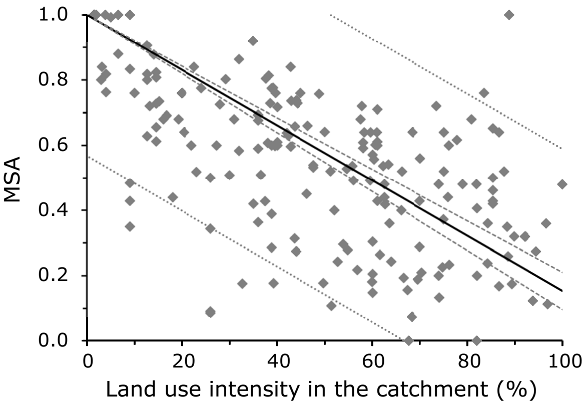


Fig. 3 – MSA in wetlands in relation to catchment land use intensity, including the regression line (black line; $R^2 = 0.23$), confidence interval (grey dashed line) and prediction interval (grey dotted line).

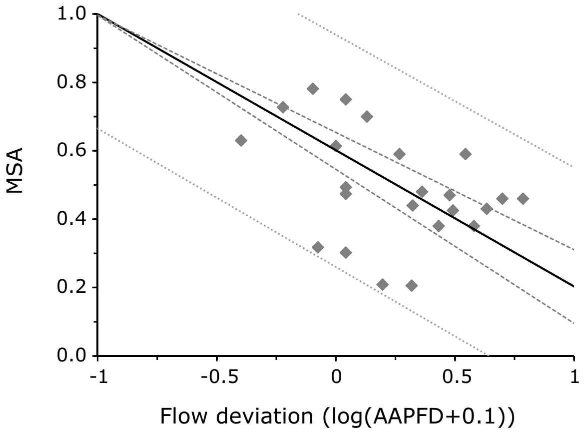


Fig. 5 – MSA in rivers and streams in relation to flow disturbance, including the regression line (black line; $R^2 = 0.1$), confidence interval (grey dashed line) and prediction interval (grey dotted line).

data. Some papers gave IBI or EQR values. The data covered a wide range of taxonomic groups: algae, macrophytes, macro-invertebrates, fishes and zooplankton. From the dataset, significant negative relationships could be derived for MSA as a function of nutrient concentrations. Logistic regression on the logarithmically transformed total phosphorus (TP) concentrations (after addition of a minimum value of 0.001 mg L^{-1}) was used, as concentrations are zero-bounded and a sigmoidal response expected. The regression has been performed for shallow and deep lakes separately; the limit has been chosen at an average depth of 3 m, crudely based on frequent dominance of submerged macrophytes and in accordance with the typology of the European Water Framework Directive. The regression line for deep lakes is below the one for shallow lakes, indicating that the original biotic community in the latter group is less vulnerable to eutrophication than the first group (Fig. 4 and Table 2). This could partly be explained by stabilizing feedback mechanisms of the submerged macrophytes that often dominate in non-eutrophic shallow lakes (Scheffer et al., 1993). Analogous data for TN were much more scarce, in conjunction with the general notion of P being considered as the main limiting nutrient for algal growth in freshwaters. There are indications, however, of a negative effect of *N* loading on biodiversity in some instances, mainly in tropical waters but also in some temperate lakes. We performed an analogous logistic regression on the *N* data (Table 2). Finally, the two relations were combined by selecting the highest value, in accordance with the limiting nutrient concept:

$$\mathrm{MSA_{nut}} = \mathrm{MAX}[\mathrm{MSA_P}, \mathrm{MSA_N}] \tag{4}$$

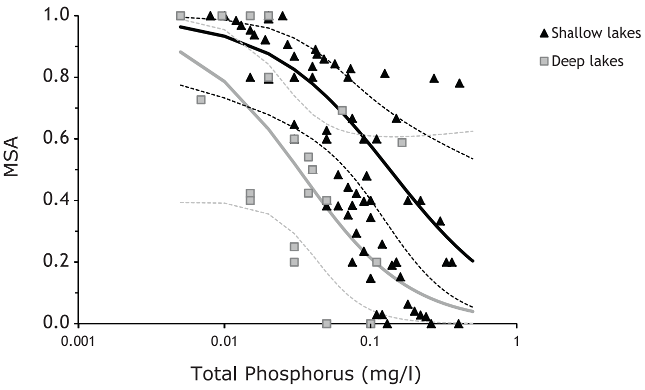


Fig. 4 – MSA in deep lakes and shallow lakes in relation to nutrient concentrations; regression lines (solid lines) and 95% confidence intervals (dashed lines).

3.1.2. *Hydrological disturbance*

Rivers: The search query resulted in 20 studies that contained usable quantitative data. The most frequently studied groups were fishes and macro-invertebrates. The results generally revealed a clear decline of MSA in response to the flow deviations (Fig. 5). A linear regression on the log 10 of the reported or estimated AAPFD (with a small value (0.1) added) has been performed, forced to 1 at zero deviation. From the graph it appears that a (moderate) flow deviation of 1 would result in an MSA value of about 0.6 and a flow deviation of 3 in an MSA of about 0.4. In the model application, the equation has been cut-off at a minimum MSA value of 0.1 for very high flow deviations.

Floodplain wetlands: For the flood dependent wetlands, 19 suitable papers (out of an initial 686) were found, from which 29 data-sets could be extracted to calculate MSA. In the majority of the cases damming was the main impact and plants the major biotic group described (for details see Kuiper et al., 2014). The cases with a low, medium and high flow disturbance had weighted average MSA values of 0.60, 0.53 and 0.46, respectively (Fig. 6). This indicates that already a moderate disturbance has a drastic impact. To incorporate this into the GLOBIO model, these values were used to fit an asymptotic exponential relation of the form $y = a \times \exp(b/(x + c))$, assigning the three categories an AAPFD value of about 0.3, 1 and 3, respectively (Table 2). The response to flow disturbance was somewhat influenced by other factors like land use in the upstream catchment, biome and taxonomical group, but the data set was too small for conclusions on subsets.

3.1.3. *Combination*

A general remark is that for all themes, only a limited number of papers presented the data in such a way that MSA values could be calculated. These papers are listed in Weijters et al. (2009), Kuiper et al. (2014) and on the website www.globio.info. The majority of these papers (over 90% of the papers on land use changes and over 80% of the ones on hydrological changes) described studies in the 'developed' part of the world: North America, Europe and Australia/New Zealand.

The derived relationships were combined by multiplying the appropriate MSA factors per water type (Table 2). The combined MSA value per pixel was calculated by area-weighted averaging of these values.

3.2. *OECD baseline scenario*

As an illustration of an application of the model chain with global scenario data, the average aquatic MSA projected for the OECD baseline is shown geographically for the years 2000 and 2050 (Fig. 7a and b) as well as the difference (Fig. 7c). Pixels without aquatic ecosystems according to the GLWD (Lehner and Döll, 2004) are shown in white on the map. According to the model, the aquatic biodiversity intactness in 2000 has already declined considerably in many parts of the world, especially in western, central and southern Europe, the USA/Mexico, south and east Asia, the southern Sahel and parts of South Africa, Argentina and Brazil (Fig. 7a). Areas like northern Europe, Canada, Russia, Australia, central Africa and large parts of South America have much less been affected. In general, the boreal biome has been affected least and the populated temperate, mediterranean and subtropical biomes most. The world averaged aquatic MSA (the average for all pixels with water bodies) has decreased to about 0.75; about three-quarters of the decline can be attributed to land-use changes (Fig. 8). As expected, the largest impacts appear in those world regions that are the most densely populated and the most cultivated. Rivers and floodplain wetlands are affected in some of the less populated catchments as well as a consequence of damming. The occurrence of algal blooms generally correlates negatively with the MSA for lakes, as can be seen from a comparison of both maps (Fig. 9a and b), which is logical as they are largely based on the same drivers in the model.

In the OECD baseline scenario, the MSA is expected to decline further in the future (Fig. 7b and c). A major decline is projected for Africa, in line with predicted changes in land use in this scenario. In Asia, Latin America and Eastern Europe further declines are also projected. A modest improvement is projected in parts of the USA, central Asia and Europe, due to an assumed stabilization of agricultural area and/or some result of eutrophication abatement. All projected MSA losses of wetlands and shallow lakes should be regarded as minimum values, as they are based on the areas presented in the GLWD (Lehner and Döll, 2004); historical wetland

Table 2 – Summary of the empirical relationships in the model.

	MSA calculations
	Land use and nutrients
Rivers	$f_{LU} = 1 - 0.0070x$ with x = human land use in catchment (0–100)
Wetlands	$f_{LU} = 1 - 0.0081x$ with x = land use intensity in the catchment (0–100)
Shallow lakes	$f_P = \exp(x)/(1 + \exp(x))$ with $x = -2.089–1.048 \times \mathrm{LN}(TP + 0.001)$; TP in mg P m^{-3} $f_N = \exp(y)/(1 + \exp(y))$ with $y = 0.2640–0.9975 \times \mathrm{LN}(TN + 0.01)$; TN in mg N m^{-3} $f_{nut} = \mathrm{MAX}(f_P, f_N)$
Deep lakes	$f_P = \exp(x)/(1 + \exp(x))$ with $x = -4.002–1.176 \times \mathrm{LN}(TP + 0.001)$; TP in mg P m^{-3} $f_N = \exp(y)/(1 + \exp(y))$ with $y = 0.145–4.768 \times \mathrm{LN}(TN + 0.01)$; TN in mg N m^{-3} $f_{nut} = \mathrm{MAX}(f_P, f_N)$
	Hydrological disturbance
Rivers	$f_{Hy} = -0.3985x + 0.60$ with $x = {}^{10}\log(\mathrm{AAPFD} + 0.1)$
Floodplain wetlands	$f_{Hy} = 0.3519 \times \exp(0.5885/(x + 1.5636))$ with $x = {}^{10}\log(\mathrm{AAPFD} + 0.1)$
	Combination
MSA per water type ('wt')	$\mathrm{MSA}_{wt} = (f_{LU}\vert f_{nut}) \times f_{Hy} \times 1$
Total MSA_{aqua}	MSA_{aqua} = Sum $(\mathrm{Area}_{wt} \times \mathrm{MSA}_{wt})$/WaterArea
	Cyanobacterial biomass (Håkanson et al., 2007)
Lakes	$B = 0.001 \times [5.85 \times {}^{10}\log(1000 \times \mathrm{MAX}(TP, 0.005)) - 4.01]\text{^}4 \times f_{TN/TP} \times f_T$; IF $TN/TP \geq 15$: $f_{TN/TP} = 1$; ELSE: $f_{TN/TP} = 1 - 3 \times [(TN/TP)/15 - 1]$; IF $T > 15$: $f_T = 0.86 + 0.63 \times ((T/15)\text{^}1.5 - 1)$; ELSE: $f_T = (1 + 1 \times (T/15)\text{^}3 - 1))$;

TP and TN in mg m^{-3}; B, cyanobacteria (mg L^{-1}); T, median surface water temperature in growing season (°C).

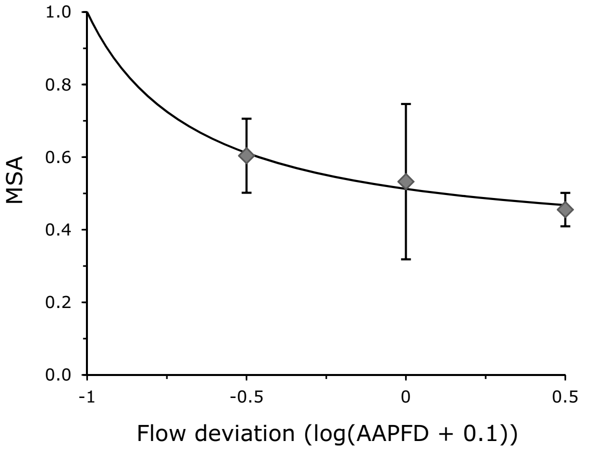
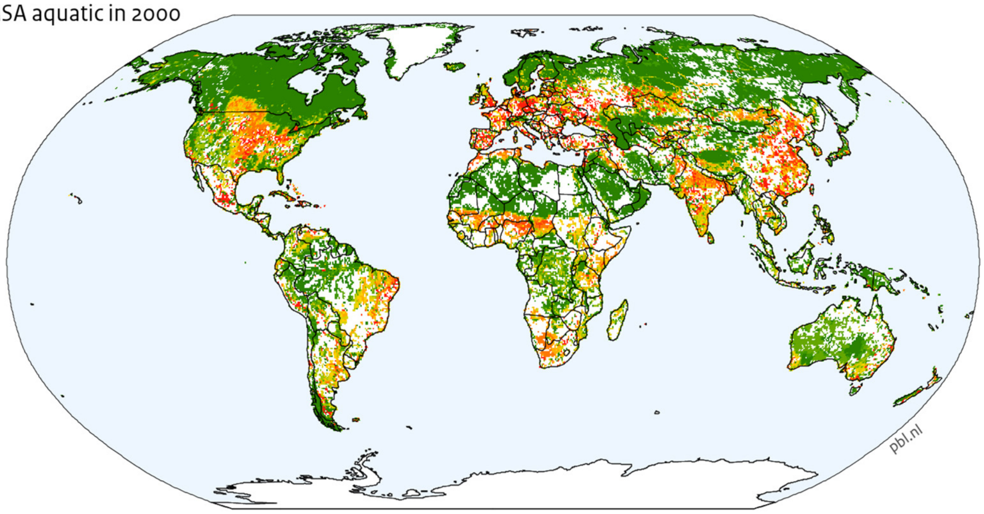
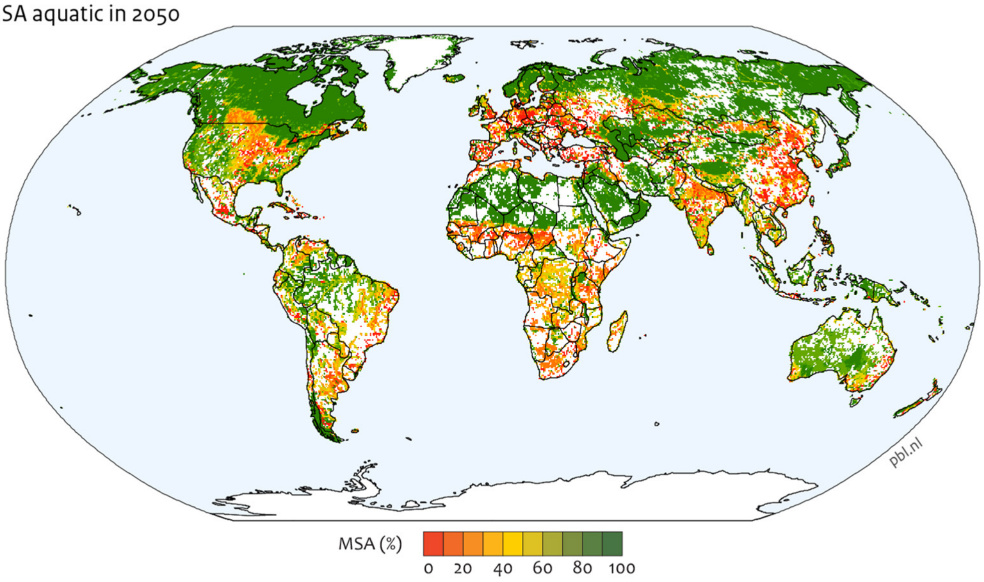


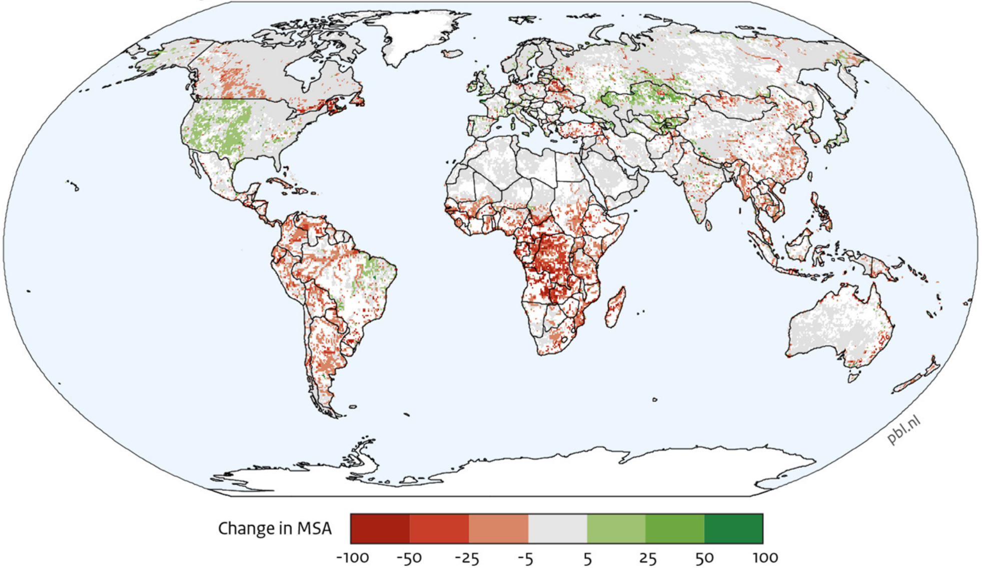
Fig. 6 – MSA in floodplain wetlands in relation to flow disturbance for three different classes of hydrological alteration (Mean effect ± Standard Error; high disturbed, N = 15; medium disturbed, N = 10; weakly disturbed, N = 4). See Kuiper et al. (2014) for a detailed description of the analysis.



a: MSA aquatic in 2000



b: MSA aquatic in 2050



c: difference 2000 and 2050

Fig. 7 – Maps of the mean freshwater MSA for (a) 2000 and (b) 2050 (OECD baseline scenario). (c) Difference between 2000 and 2050. (Areas without water according to the GLWD are shown in white.)

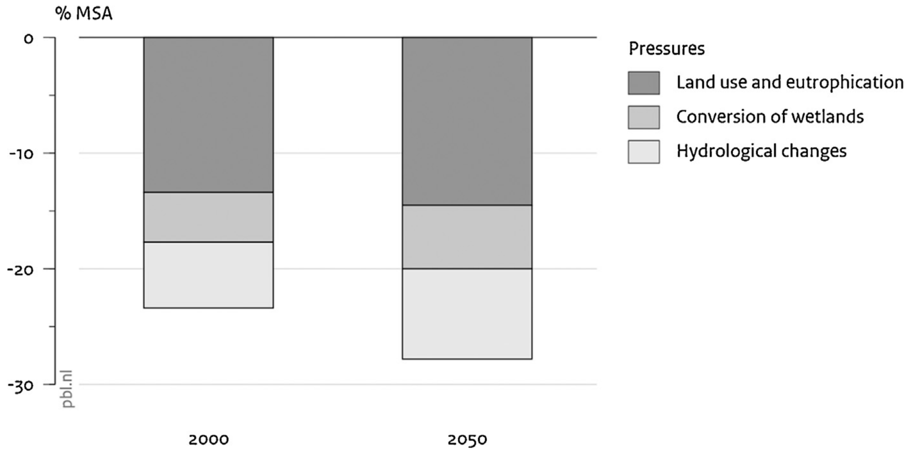


Fig. 8 – World-averaged aquatic MSA loss in 2000 and 2050 according to the OECD baseline scenario and contribution of the main pressures included in the model.

conversions are not accounted for in the calculations and future conversions only as a minimum estimate.

4. Discussion

This study shows that biodiversity intactness in freshwater ecosystems, measured as MSA, is negatively related to two dominant categories of anthropogenic stressors, i.e. (1) land-use and eutrophication in the catchment (affecting 'water quality') and (2) hydrological disturbance by dams and/or climate change (affecting 'water quantity'). This conclusion can be drawn qualitatively from the ensemble of case studies, and underpinned quantitatively by the meta-analyses on the data of a subset of these papers. This conclusion holds for the major types of inland aquatic ecosystems: rivers, lakes and wetlands, while wetlands are also directly affected by conversion and drainage. In general, standing water bodies in heavily used catchments loose about 80% of their original species composition and running waters about 70%. Severe hydrological disturbance causes a decline of 60–80% of the original species composition in running waters and more than 50% of it in connected wetlands.

This pattern was derived by scaling up and combining a number of local/regional case studies. The variation of observed effects between individual cases is large – as might be expected both from the variation in local (e.g. morphological, geochemical) and regional (e.g. hydrological, geomorphological and climatic) features of the sites, and also from the 'composite' nature of the discerned drivers. The driver 'human land use' for instance is made up of many composite factors (eutrophication, erosion/sedimentation, riparian settlements and others) that alone or in combination affects biota. As in practice several of these underlying factors will be correlated, we argue that this way of scaling up different cases is acceptable for obtaining a broad picture. The cases were selected under the condition that they had evaluated sites or periods comparable with respect to natural factors such as climate, geomorphology, stream order, catchment size and water chemistry. As for the hydrological disturbance, we chose the degree of deviation from the natural seasonal flow pattern as the crucial variable (Poff et al., 1997). This deviation may have a different nature in different systems, e.g. increased flow variation in naturally steady rivers, versus decreased variation in naturally dynamic ones.

The quantitative results of this modelling exercise should be regarded as indicative as they are based on only a limited set of case studies. Many studies could not be used because data were presented inadequately. In addition, there is a substantial bias geographically towards case studies from North America, Oceania and Europe, although the absence of a reference situation was often a problem in the latter region. The boreal and also some of the tropical regions were underrepresented because they are (until now) less disturbed, and generally less studied. An overall constraint is that only (data from) peer-reviewed papers were included, which also tends to overemphasize studies from the developed part of the world. An extension of the search with grey literature (combined with a basic data quality check) would broaden the results.

An important cause of the data limitation arises from the fact that primary data on species composition, required to compute the MSA indicator, have often not been published. Increasing journal facilities as well as ongoing projects for international data compilation such as the Global Biodiversity Information Facility GBIF (www.gbif.org) and BioFresh (www.freshwaterbiodiversity.eu) will probably lead to an increase in suitable data in the near future. Data not usable as input might be appropriate for validation purposes. An increase of the number of cases would of course not reduce the total variability in the data set, which should be taken as unavoidable. Still, it would reveal possible differences in sensitivity between biomes or ecotypes, which could then be used to refine the model. In the meantime, the model could serve to fill the 'data gaps' by extrapolating relations from other ecotypes.

Despite these limitations, the model has shown to produce plausible results at the level where it was meant for, i.e. the impact of broadly-defined drivers at the scale of relatively large regions and catchments. It informs policy makers at the global level in what regions aquatic biodiversity is expected

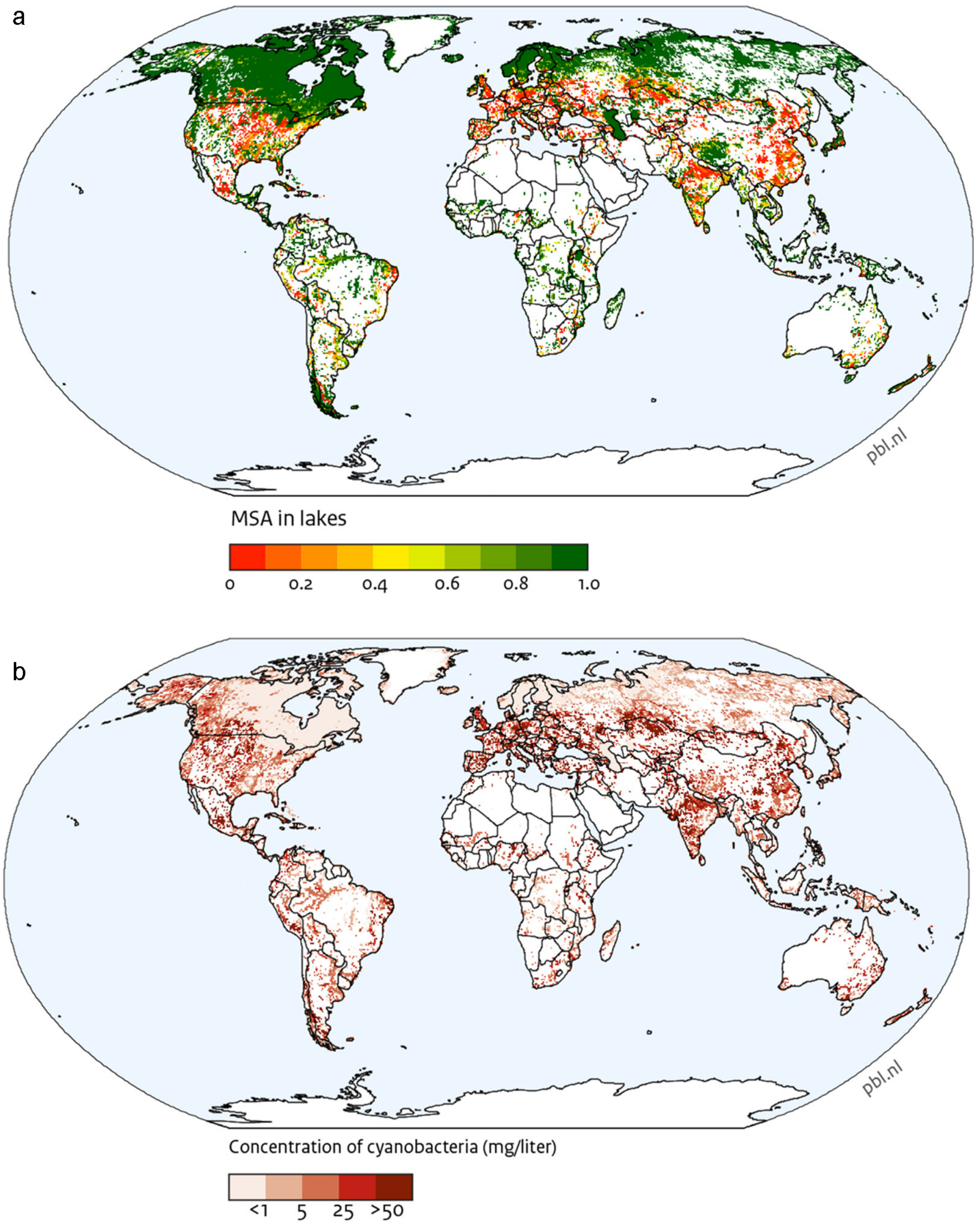


Fig. 9 – (a) Projected MSA values and (b) harmful algal blooms (cyanobacteria) concentration in lakes for the year 2000.

to be affected most and by what causes. Scenarios on global issues like population growth, food demand, agricultural production, sanitation and wastewater treatment and energy mix can be linked to the ecological intactness of ecosystems in world regions. This makes biodiversity – on a broad scale – 'modelable' (linkable to these global environmental drivers) and provides one of the tools to evaluate the CBD biodiversity targets (CBD, 2014). In this way it complements the GLOBIO sister model for terrestrial ecosystems (Alkemade et al., 2009). The GLOBIO approach has contributed to the awareness that the CBD biodiversity targets for 2010 were not met, by performing a number of global scenario studies (Ten Brink et al., 2010; OECD, 2012; PBL, 2014).

The GLOBIO-Terrestrial model covers the drivers land-use change, infrastructure/fragmentation, atmospheric nitrogen deposition and climate change, by adding an important category of ecosystems and specific aquatic drivers (such as the water–food–energy nexus). Both models reveal some parallel results for the effects of human land-use: the densely cultivated regions of the world come out as the most affected, but in the aquatic model the spatial pattern in the MSA is influenced by the connectance of pixels within river catchments. Moreover, the effects of flow disturbance are also seen in some less-populated regions. The terrestrial GLOBIO model reports an average world-MSA around 0.7 in 2000 and 0.63 in 2050. Our model gives comparable figures (about 0.75 and 0.7), but these values are certainly an overestimation in many regions, as historical wetland conversion was not accounted for and not all drivers were included. Both models lack the impact of exotic species invasions. Because of the relatively higher number of lakes and wetlands in the boreal regions, this biome (which is in general the least populated) has more influence on the world-average for GLOBIO-Aquatic than for GLOBIO-Terrestrial.

Many of the most-impacted world regions according to GLOBIO-Aquatic also appear from the model of global threats to river biodiversity by Vörösmarty et al. (2010). Besides, these authors conclude that in the developing world, the regions with a high threat to river biodiversity often coincide with those where water availability to humans is at risk.

We consider the MSA a useful indicator for the state of an ecosystem, as it reflects the intactness of the native species composition and allows comparison of different systems on the same scale. It is also an 'objective' indicator in that it uses the same baseline for all ecosystems and regions, which contributed to its acceptance in the policy arena. However, MSA is by no means the only indicator of biodiversity. Other indicators like species richness, Shannon–Wiener index and evenness provide other kinds of information and show partly different responses to disturbance than MSA. In moderately disturbed situations, the decrease of original species is often accompanied by the appearance of 'newcomers' (the 'intermediate disturbance hypothesis'), thereby increasing species richness. This is also in line with the unimodal ('hump-shaped') species richness curves often found in relation to productivity and other factors (Leibold, 1999; Declerck, 2005). Some of the newcomers may be invasive species. This is only reflected in the MSA if the newcomers lead to the decline of native species, which is not necessarily the case.

Defining the 'undisturbed' (or 'pristine') state of an ecosystem when calculating the MSA is often difficult. Truly pristine aquatic systems are rare, but we took a pragmatic approach by following the definitions of 'least disturbed systems' in the case descriptions in the literature used as reference systems for the driver under concern. When comparing the biota at natural and disturbed situations, we implicitly assumed that the time since the disturbance had been sufficiently long to observe the changes in biota. In many cases, the ecosystem might still be in a transient state, e.g. species that are about to disappear in the long run are still present in the first years. A related topic is that we were not able to distinguish possible hysteresis effects between an increasing disturbance and a decreasing one (restoration), as has for instance been shown for eutrophication of lakes (Scheffer et al., 1993).

A general concern about scaling up species composition data is that the relationships with the drivers may differ across scales. The correlation between a certain driver and local diversity may not hold at the regional level. We accounted for this by comparing only data that covered the same scale as far as possible. Besides, this problem plays less a role in our study because we used an indicator of intactness (or naturalness) based on original species only. This indicator is probably less sensitive for this scale issue than 'absolute' biodiversity indices like species richness. Averages of indicator values calculated per pixel over larger regions (multiple pixels) should be interpreted with care. This holds for MSA values as much as for more 'absolute' indicators. For example, on a larger scale, local decrease or extinctions of species might be compensated by increases elsewhere, and species may migrate within the region. The averaged value will be different from a value that would have been calculated for the region. Nevertheless, the averaged value does give an indication of how much of the (in this case aquatic) ecosystems in the region lost their original species composition. It does not indicate, however, the absolute number of species under threat in different regions, as the MSA is scaled to 1 for all studies, i.e. naturally species-rich and species-poor systems are treated in the same way. It is possible, however, to weigh the MSA values by the natural species richness per biome, as has been demonstrated for the GLOBIO-Terrestrial model.

Our approach should hence be regarded as complementary to other approaches and indicators. Indicators like the Living Planet Index (LPI) (Loh and Wackernagel, 2012) and the Red List Index (RLI) (www.iucnredlist.org) provide information on the (global) trend in selected species groups, but are difficult to link to environmental models. Another approach are the ecological assessment methods derived at the European-scale (Moss et al., 2003; Penning et al., 2008; Verdonschot and Nijboer, 2004 and others), which derived indicator species for certain disturbance factors. Azevedo et al. (2013) related relative species richness for several biotic groups to total phosphorus concentrations in lakes and streams worldwide. Although methods and indicators differ, these studies also support a decrease of biodiversity at higher nutrient levels. Important is also the relation between these structural and more functional indicators of ecological integrity, like food web structure, boundaries for regime shifts of vulnerable ecosystems and delivery of ecosystem services (Pereira et al., 2013). However, Özkundakci et al. (2014) found only weak relations between different types of indicators in deep lakes in New Zealand. Further model development will probably require combinations of different modelling techniques (cf. Mooij et al., 2010); besides meta-analyses of case studies these could include process-based modelling (e.g. for factors like exploitation and for functional indicators), or qualitative reasoning if data are not there. These topics will be addressed in future versions of the model.

Some other, more 'internal', issues need to be considered when evaluating the model. We have treated the impacts of the different categories of drivers as independent (hence we multiplied the factors). We consider this a reasonable assumption, as the drivers were treated separately in the underlying case studies. Interactions between drivers can, however, not be excluded, both synergistically and antagonistically. There is a weak indication of wetlands in intensively-used catchments being somewhat less sensitive to hydrological disturbance. A synergistic effect is sometimes found between invasive species and other disturbances, but the current dataset was too limited to show that.

Another issue is whether the effect of a driver is modified by other factors. We explicitly separated the regression analyses per main water type (i.e. river, wetland, shallow lake, and deep lake) (see Table 2 and Figs. 2–6). Other 'effect modifiers' were in some cases taxonomic groups; e.g. in rivers, fishes were more vulnerable than macro-invertebrates, while in wetlands, amphibians tended to be relatively sensitive and animals generally more sensitive than plants. In line with this is also our finding that shallow lakes, often dominated by submerged macrophytes, were less sensitive than deep lakes. One could speculate that the vulnerability of aquatic animals might have to do with the complex life cycle of many species, or with limited possibilities to escape unfavourable habitats, while dispersal of plants might be more easy. These aspects can be further investigated when more data will become available.

To conclude, we presented a model approach that is able to link aquatic biodiversity intactness to spatially explicit models of global environmental drivers, and that allows for scenario analyses to inform policy makers at the global level in which regions the aquatic biodiversity is impacted most by environmental pressures. Although still in development and hampered by data deficits, we feel that the approach is promising and can successfully be improved when data will be increasingly available.

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