IMPACT

Developing an integrated model to predict abiotic habitat conditions and biota of rivers for application in climate change research and water management

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WFD article targeted

Article 11 on the Programme of Measures was targeted by assessing the effect of large scale pressures on river restoration success including climate change.

Key words

Water Framework Directive, climate change, environmental change, river restoration, modelling, fish, macroinvertebrates

Project objectives

- Develop and test an integrated modelling framework to predict the habitat conditions and to identify the main limiting pressures for biota of rivers.
- Assess the effect of large scale pressures (climate and land use change) on river biota and on the effects of reach-scale restoration measures.
- Consider for the first time interacting effects of (i) abiotic habitat conditions, (ii) dispersal abilities of species, and (iii) the species pool available for (re-) colonization.

Policy focus

- At the operational level, the project provides an approach to more realistically assess the effect of reach-scale restoration measures given the anthropogenic pressures at larger spatial scales and to identify effective measures at the river network and catchment scale. For the first time, this assessment includes missing source populations and impacts of migration barriers.
- At the strategic level, the project’s modelling framework provides empirical evidence that neither predicted climate change nor land use changes will impact on river discharge and water quality to an extent that principally hampers river rehabilitation and that could not be mitigated.

Policy milestones and relevant projects key outputs

- Modelling framework: The modelling framework developed integrates: (i) an ecohydrological model describing catchment scale pressures and processes (e.g. discharge, nutrient loads), (ii) a 2D hydrodynamic model predicting the hydraulic habitat conditions at the reach-scale for discharges modelled by the ecohydrological model for different scenarios, (iii) habitat models assessing the suitability of the hydraulic habitat conditions for biota, (iv) morphological models assessing if the predicted discharge changes significantly affect river morphology, habitat conditions, and in turn biota, (v) species distribution and dispersal models predicting the species pool available for (re-) colonizing the habitats, (vi) interaction models considering the feedback of biota on the abiotic habitat conditions. Finally, information on physical habitat conditions, water quality, and the species pool are combined to assess the effect of the different pressures on biota.
• **Novel models:** The first GIS based fish dispersal model (FIDIMO) was developed to predict species-specific dispersal probabilities of fishes, while considering adverse effects of migration barriers and missing source populations (Radinger et al. 2013). Moreover, a novel habitat model for invertebrates (Habitat Evaluation Tool) was developed that is able to predict species abundance besides species presence (Kiesel et al. 2014).

• **Case-study application:** In two case-study catchments, a near-natural study reach was selected as analogue for the habitat conditions of a typical restored reach. The effect of different climate change and land use change scenarios was modelled on discharge, river morphology, hydraulic habitat conditions, habitat suitability, and biota to (i) compare the potential effect of different pressures, and (ii) investigate if large scale pressures constrain the effect of reach-scale restoration measures.

• **Importance of habitat conditions vs. species pool:** Habitat suitability for fish indicated that all target species have similar probabilities to establish in a restored reach with comparable habitat conditions; however, their recovery strongly depends on the distance to the nearest remnant population and their species-specific dispersal ability. Thus, species may strongly differ in respect to the time needed for reaching and colonizing a restored river reach.

• **Inference of empirical dispersal parameters:** Coupling traditional population genetics analyses, multi-specific empirical genetic data gathered at a large spatial scale and genetic data simulated under different competing dendritic meta-population models allowed us to obtain valuable information concerning the overall dispersal capacities (dispersal rates, dispersal directionality and dispersal distances) of four fish species at different spatio-temporal scales.

• **Importance of source populations vs. migration barriers:** The dispersal models revealed that re-colonization of restored reaches is potentially more strongly affected by missing source populations than by migration barriers. Therefore, it is recommended that river management should focus on source populations which have not been adequately considered in the past, besides restoring river continuity.

• **Effect of discharge changes on fish:** In both case-study catchments, the climate change scenarios predicted a substantial decrease in discharge, which resulted in modified hydraulic habitat conditions that caused small to moderate, species-specific changes in the habitat suitability for fish. The habitat model predicted non-linear effects of discharge changes on habitat suitability, both negative and positive. It is concluded that climate change might constrain the effect of river restoration for some fish species but does not limit restoration success in general.

• **Effect of changes in nutrient concentrations on invertebrates:** In the land use and climate change scenarios, the moderate changes in invertebrate abundance reflect the predicted moderate changes in nutrient concentrations. Most species occurring in the modelled lowland catchment are nutrient tolerant and are predicted to decrease in abundance with decreasing nutrient concentrations.

• **Modelling framework applications:** The application of the integrated modelling framework in IMPACT has focused on hydraulic habitat conditions for fish and nutrient loads for invertebrates. However, other environmental variables can be easily included and hence, the integrated modelling framework applied for various research questions in river ecology.
Limitations identified by the project

- The application of the modelling framework showed that abiotic and biotic models can be successfully linked to predict river biota. The following main research needs were identified:

  Need to refine biotic models: The precision of the output of the abiotic models is higher than what presently can be used for the biotic models, and hence the overall output of the modelling framework could be enhanced by refining the biotic models.

  Abiotic models should focus on biologically relevant parameters: Model predictions could be enhanced if abiotic models focus more on habitat parameters relevant for biota, especially on sediment sorting and resulting sediment sizes, and organic substrates including macrophytes and their feedback on abiotic habitat conditions (“ecosystem engineers”).

  Limited knowledge on habitat preferences and dispersal abilities: The knowledge on habitat preferences and suitability is still limited, often based to expert judgement, and hence, empirical studies are needed for fish and invertebrates. Moreover, missing empirical data on the dispersal abilities of macroinvertebrates limits the applicability of dispersal models.

Main recommendations

- The relationship between abiotic habitat conditions and their effect on biota is non-linear, i.e. predictions cannot be solely based on abiotic habitat variables, but also on biotic interactions.

- Uncertainty of the modelling results is still considerably high and hence, river restoration and the Programmes of Measures should follow an adaptive management approach, i.e. the effect of the measures should be monitored and the measures adjusted accordingly.

- Large-scale pressures potentially constrain the effect of restoration measures and should be adequately considered in the Programme of Measures. In the case-study applications, results indicated that discharge changes due to climate change are of minor importance, and restoration success more strongly depends on large-scale pressures like nutrient loads and missing source populations. However, this might be different in other catchments.

Further information on project:


- Participating countries and institutions:

  - Leibniz-Institute of Freshwater Ecology and Inland Fisheries (coordinator, Germany)
  - University of Duisburg-Essen, Department of Aquatic Ecology (Germany)
  - Christian-Albrechts-University Kiel, Department of Hydrology and Water Resources Management (Germany)
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Further information:

- Website: http://www.impact.igb-berlin.de/
- Fish dispersal model FIDIMO: http://grasswiki.osgeo.org/wiki/AddOns/GRASS_6#r.fidimo
- FISHMOVE tool to quantify fish migration distances: http://cran.r-project.org/web/packages/fishmove/index.html
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1 Introduction

River biota is affected by anthropogenic pressures that act at different spatial scales (Fig. 1), ranging from global and catchment scale hydrological changes due to climate or land-use change, point source pollution, and diffuse source pollution like nutrients, pesticides, and fine sediment, to reach-scale hydromorphological alterations like channelization. Besides these changes of the physical habitat conditions, biota of rivers depend on the species pool available for (re-) colonization. Sensitive species of the natural species pool are often rare or extinct in the catchment or region, limiting the number of source populations. Moreover, migration barriers restrict (re-) colonization of newly restored habitats or river reaches depopulated by natural or human-caused calamities.

Several empirical studies indicate that large-scale pressures like catchment land-use can be more important in shaping invertebrate and fish communities compared to pressures at smaller spatial scales (Roth et al. 1996, Allan et al. 1997, Black et al. 2004, Hughes et al. 2008, Stephenson and Morin 2009, Sundermann et al. 2013). They might even limit invertebrate and fish assemblages (Wang et al. 2007, Bryce et al. 2010, Kail et al. 2012), especially in heavily modified rivers (Kail and Wolter 2013), and hence, potentially govern river biota and constrain the effect of reach-scale river restoration measures. It is inherently difficult to infer causal relationships based on such empirical studies and statistical analysis since variables often show high co-linearity and are proxies for different pressures. Complementary modelling could help to assess the importance of
different pressures by coupling models that predict the effect of these pressures on abiotic habitat conditions and biota.

Most modelling approaches to predict biota of rivers focus on the hydromorphological conditions at the reach or river segment scale and on habitat suitability. In the widely used microscale habitat models, the hydraulic microhabitat conditions (e.g. flow velocity and depth, substrate) are predicted using a hydraulic model, and habitat suitability is assessed based on environmental-biological relationships (Harby et al. 2004, Conallin et al. 2010). In mesoscale habitat models, channel features like riffles are mapped, probability density functions of microhabitat conditions for each mesohabitat are derived from statistical analysis, and meso- as well as microhabitat descriptors are used to assess habitat suitability based on environmental-biological relationships (Dunbar et al. 2011). There are only few integrated modelling frameworks which also consider large-scale pressures at the global, catchment or river network scale besides the reach and segment scale habitat conditions, like the first application of coupling hydrological and hydrodynamic models by one of the project partners (Kiesel et al. 2009).

The overall aim of this project was to further develop and test an integrated modelling framework to predict the abiotic habitat conditions and to identify the main limiting pressures for biota of rivers. Based on the work of one of the project partners (Kiesel et al. 2009), such an integrated modelling framework was developed to predict the abiotic habitat conditions, habitat suitability, as well as the species pool available for (re-) colonization of these habitats (Fig. 2). This information can finally be used to assess which species potentially can become established in a specific river reach. In this modelling framework, the following pressures and spatial scales were considered:(i) global scale climate change, (ii) catchment scale land use changes, (iii) the species pool available for (re-) colonization, (iv) hydromorphological alterations (including migration barriers) in the up- and downstream river network, as well as (v) the local hydromorphological state and the resulting habitat conditions at the reach scale (see section for a more detailed description of the integrated modelling approach).

Software tools were readily available for some of the models (e.g. ecohydrological, hydrodynamic models), but some of the models first had to be developed, especially dispersal models for fish and invertebrates (section 2.1) and a novel habitat model for invertebrates (section 2.1).

After developing the novel modelling tools and the integrated modelling approach, it was applied and tested in two case-study catchments: The lowland, sand-bed Treene River in Northern Germany, and a gravel bed river in south-western France (Célé) (the originally planned modelling of the third case-study catchment was not finalized for the reasons given in section 2.2). In the Treene and Célé catchment, a near-natural study reach was selected as an analogue for the habitat conditions which can be expected to result from typical projects restoring natural channel dynamics at the reach-scale (study reach in Fig. 1).

The modelling framework was applied (i) to assess the effect of discharge changes due to climate- and land-use change along the model chain of the ecohydrological, hydrodynamic, and habitat models on the habitat conditions and biota of the study reach, and (ii) to compare it to the effect of other pressures like nutrient pollution and restricted (re-) colonization potential, and assess to what extend large-scale pressures potentially constrain the effect of reach-scale restoration measures.
2 Methodology

2.1 INTEGRATED MODELLING FRAMEWORK

(IGB, UDE, CAU)

In the following, the integrated modelling framework (Fig. 2), which was developed in the IMPACT project based on the work of one of the project partners (Kiesel et al. 2009), will be described. The integrated modelling framework and the novel habitat model for invertebrates and dispersal model for fish are rather important results than simply methodological aspects. For the sake of brevity and since it better fits in the usual order of presenting scientific research, these results are included here in the materials and methods section. More detailed information on the integrated modelling framework, the invertebrate habitat model, and fish dispersal model are given in Kail et al. (in prep.), Kiesel et al. (2014), and Radinger et al. (2013).

First, an *ecohydrological model* is used to predict water quantity and quality. Catchment data on climatic variables, land use, soil types, topography, and point sources are needed to predict discharge, suspended sediment, and nutrient loads along the river network. First, an *ecohydrological model* is used to predict water quantity and quality. Various models are available, which can be categorized based on an increasing spatial discretisation and computational demand: (i) lumped models aggregate the input data within (sub-)basins (e.g. HBV, Bergström...
1976, 1992), (ii) semi-distributed models divide these (sub )basins into areas of equal properties (e.g. AGNPS, Young et al. 1989, BlueM, Reußner et al. 2009, SWAT, Arnold et al. 1998), and (iii) distributed models are mostly grid based and solve the internal algorithms for each single model grid cell (e.g. SHETRAN, Ewen et al. 2000, GSSHA, Downer and Ogden 2004, WASIM-ETH, Schulla 1997).

Semi-distributed models like SWAT are most suitable for application in the modelling framework since they combine reasonably fast execution times, which enable auto-calibration and multi-scenario runs, with the capability to assess the impact of spatially explicit land use changes at defined locations in the river network. SWAT requires spatially distributed data on climate, land use, soil, topography, point sources, and the river network. For calibration and validation, data on discharge, water quality, and suspended sediment loads are needed for longer time-periods, ideally daily data including a wide range of hydrological extremes (e.g. flood and drought years).

Second, a **1D hydrodynamic model** is used to predict the water level at the downstream end of the study reach, which is a necessary input for the subsequent 2D hydrodynamic model, based on an existing rating curve of a downstream gauging station. 1D hydrodynamic models numerically solve basic equations for conservation of water mass and water flow momentum to calculate flow velocity, depth, shear stress, and water level spatially averaged over cross-sections (i.e. one-dimensional) along rivers. Such models are standard in hydraulic engineering, many software tools are available as freeware, and any of them could be used for application in the modelling framework (e.g. BLTM, Jobson 1997, BRI-STARS, Molinas 2000, CCHE1D, Wu and Vieira 2002, HEC-RAS, USACE 2010). For setting up the 1D hydrodynamic model, data on cross-section form for a number of cross-sections between the gauging station and study reach are needed, as well as flow velocity and depth to back-calculate roughness.

Third, a **2D hydrodynamic model** is used in the modelling framework to predict the hydraulic habitat conditions (e.g. flow velocity, depth, shear stress) for each grid cell of the computational grid covering the study reach based on the discharge and water level at the downstream end coming from the ecohydrological and 1D hydrodynamic model, respectively, as well as information on channel bathymetry. 2D hydrodynamic models numerically solve the basic mass conservation equation and two horizontal components of momentum conservation to calculate two horizontal flow velocity vectors and flow depth for each node of a two-dimensional computational grid covering the study reach. 2D hydrodynamic modelling is standard in hydraulic engineering and many commercial models but also freeware is available like TELEMAC-MASCARET (Hervouet and Bates 2000), CCHE2D (Jia and Wang 2001), RIVER2D (Steffler and Blackburn 2002), ADH (Berger et al. 2013), and the iRIC software package (http://i-ric.org). They require channel bathymetry and roughness as input, as well as water level and discharge as boundary conditions. Moreover, 2D morphodynamic models can be used to model sediment transport and the resulting substrate distribution.

Fourth, **habitat models** are used to assess the suitability of the hydraulic habitat and substrate conditions predicted by the 2D hydro- and morphodynamic models based on habitat preferences of the species.

For fish, **conventional habitat models** are used in the modelling framework to assess the suitability of the habitat conditions in the study reach, as well as seasonal changes. Conventional habitat models quantify the suitability of a habitat for specific species based on univariate relationships between species presence and single habitat parameters (mostly hydraulic parameters, e.g. depth, velocity). These so-called habitat suitability curves are either based on expert opinion or empirical
observation of habitat use (habitat utilization curve), corrected for habitat availability (habitat preference curves) (Bovee et al. 1998). Available habitat conditions are compared to the preferred habitat conditions described by the habitat suitability curves, which yields a habitat suitability index ranging from 0 (unsuitable) to 1 (most suitable). However, several species don’t show clear habitat preferences due to opportunistic resources use and broad environmental tolerances. Fuzzy logic models consider that the information on habitat suitability is often imprecise (Ahmadi-Nedushan et al. 2006, Mouton et al. 2007) by not dividing the habitat variables (e.g. flow velocity) into distinct classes (e.g. low, medium, high) but using fuzzy membership functions which allow to assign a specific value to more than one class. Habitat suitability of combinations of habitat parameters are then assessed using fuzzy-logic rules based on expert judgement (e.g. “IF velocity IS low AND depth IS high THAN suitability IS high”), and a final de-fuzzification process allows to give quantitative values. Habitat suitability is usually assessed for each modelled unit (e.g. each node of the 2D hydrodynamic model computational grid), values are weighted by area of the units and summed, resulting in the Weighted Usable Area (WUA, Bovee and Cochnauer 1977, Payne 2003), a single value for the whole study reach.

Several habitat suitability models are available like PHABSIM (Milhous et al. 1984) and CASiMiR (Jorde 1996) and they have been extensively used for modelling riverine fish (e.g. reviewed by Hardy 1998, Kerckhove et al. 2008, Nestler et al. 1989) but also macroinvertebrates (Gore et al. 2001, Gore 1989). The models use information on habitat conditions and habitat needs as input to quantify the WUA but information on the WUA necessary for a species to establish is missing, and hence, species’ presence and abundance cannot be directly predicted based on the habitat conditions.

For invertebrates, a novel Habitat Evaluation Tool has been developed for the modelling framework by Kiesel et al. (2014), which was enabled by a large dataset containing substrate-specific abundance data that have been collated in recent years. The Habitat Evaluation Tool (HET) uses these empirical data to predict the presence and abundance of invertebrates in a specific river reach. The method consists of three consecutive steps: First, an empirical generating dataset is used to calculate (i) the mean total abundance of all species on each substrate, and (ii) the mean abundance of each single species on each substrate. Second, a large number of virtual “electronic” samples are taken from each substrate (following Lorenz et al., 2004), i.e. random draws from all individuals of all species occurring on a substrate with the number of draws equal to the mean total abundance. Third, the substrate-specific virtual samples are weighted according to the area actually covered by the substrate in the study reach, and the resulting composite taxalist can be used to calculate biological metrics.

In contrast to the seasonal changes of the habitat conditions (e.g. monthly values of WUA for fish), the effect of these seasonal changes on the presence and abundance of species hardly can be modelled since it depends on numerous processes like e.g. the loss of individuals by catastrophic drift. However, based on the empirical data, it is possible to predict the presence and abundance in general and over longer time periods including at least one reproductive cycle. In principle, the method can also be applied using other habitat parameters than substrate and multiple habitat parameters (e.g. substrate and flow conditions). However, available habitat specific sampling data are mostly restricted to substrate-specific samples.

The morphological models have been added to the modelling framework for two reasons: First, morphological models were used to model the dynamic equilibrium channel morphology to compare it to the bathymetry mapped in the field. The mapped state might be in disequilibrium (not adapted to the governing controls like the imposed water discharge), only reflecting the conditions
found during the field campaign and not being representative for the long term morphological and habitat conditions. In case the mapped bathymetry strongly differs from the equilibrium state, it might be more reasonable to use the modelled equilibrium bathymetry to predict the habitat conditions and assess habitat suitability. Second, morphological models were used to predict the effect of discharge changes on channel morphology in the different climate- and land-use scenarios. In general, channel morphology adjusts to the imposed water discharge, sediment load, and sediment properties (e.g. bed and bank material). Alterations of these controls like increased urban runoff or high flows due to climate- and land-use change can cause channel instability (Knighton 1984). These morphological changes in turn affect channel hydraulics, habitat conditions and suitability. Presently, there is no physical-based morphodynamic model available to predict the dynamic equilibrium state and long-term evolution (but see recent progress towards such a model in Asahi et al. 2013). Alternatively, the effect of discharge (changes) on different aspects of channel morphology (channel geometry, planform, bathymetry) was modelled in three consecutive steps.

**Channel geometry** (width, depth, slope) can be predicted using three different approaches: (i) Empirical hydraulic geometry equations (regime equations) are statistical relationships derived from observed channel geometry and explanatory variables like bankfull discharge (e.g., Leopold and Maddock 1953), river bed grain size (Bray 1982, Andrews 1984), silt/clay content of bank material (Shields 1996, Schumm 1971), and riparian vegetation (Hey and Thorne 1986, Andrews 1984). Regime equations are practical tools but purely empirical and hence, restricted to the region they were developed in and give no insight in the governing processes. (ii) In regime models, a set of equations, which usually includes equations on continuity, flow resistance, and sediment transport, is numerically solved to calculate channel geometry (Chang 1979, 1980, Yang et al. 1981, White et al. 1982). Typically, the input data include formative discharge, channel roughness, grain size, and sediment load. Models also including the effect of bank strength more precisely predict channel geometry (Millar and Quick 1993, 1998, Millar 2005, Eaton et al. 2004, Eaton 2006). The indeterminate set of equations is solved using an extremal hypothesis, where it is assumed that rivers develop towards a stable channel form (dynamic equilibrium) where a specific parameter is maximised or minimised, e.g. stream power is at the minimum necessary to transport the imposed water and sediment discharge. The extremal hypothesis is sometimes considered a workaround which lacks a physical basis (Griffiths 1984, Ferguson 1986, Darby and Thorne 1995, Mosselman 2000). (iii) Somewhat more physically-based approaches remain empirically calibrated (Parker et al. 2007, Wilkerson and Parker 2011), and hence, are difficult to apply in the presented modelling framework.

**Channel planform** changes of freely meandering rivers (meander migration, lateral channel dynamics) can be modelled using a meander migration model. The physical-based dynamic models can be classified according to the migration processes considered. In all models based on the first dynamic model of Ikeda et al. (1981), bank retreat is caused by fluvial entrainment of bank material due to excess flow velocity (e.g. Parker et al. 1982, Parker 1984, Abad and Garcia 2006). Other models do also consider mass failure due to excess water depth (Crosato 1989, 2008, Odgaard 1989) and the deposition of failed bank material at the bank toe in a more mechanistic bank erosion submodel (Darby et al. 2002). Virtually all models assume that bank accretion in the inner meander bend equals bank retreat at the outer bend, i.e. channel width is considered constant (Crosato 2007) and a necessary input, coming from the regime equation or model (Fig. 2). Other necessary input data are formative discharge, channel roughness, grain size, and bank erodibility.
Channel bathymetry can be modelled using standard 2D or 3D morphodynamic models that solve equations on water motion, conserving mass, momentum, and sediment fluxes, and - from the divergence of these fluxes – bathymetry iteratively. Often-used codes are Mike21 (Enggrob and Tjerry 1999), Delft3D (Lesser et al. 2004), Telemac and various research codes (e.g. Jang and Shimizu 2005). A powerful characteristic that was useful to the present study is that the bathymetry and bar patterns emerge from the underlying physics and the grid shape or a perturbation on the bed, and bars appear with wavelengths in agreement with analytical bar theory (Schuurman et al. 2014). This means that these models are insensitive to grid resolution and other numerical aspects, whilst they are sensitive to the initial- and boundary conditions which is useful here to predict pattern changes from changing boundary conditions. Models including Large Eddy simulation, which is an advanced method for spatially non-uniform turbulence closure, give more accurate results in sharp meander bends and hence, are especially suited for heavily meandering rivers (e.g. Delft3D).

Dispersal models were considered in the integrated modelling framework since biota of rivers not only depends on habitat conditions and habitat suitability but also on the availability of individuals to colonize these habitats. Dispersal models are used to assess the effect of a limited species pool for (re-) colonization, caused by missing source population and migration barriers, on species composition in the study reach. Dispersal modelling consists of two steps: (i) the location of source populations in the river network is predicted using species distribution models, and (ii) the spread or dispersal from each source population is modelled based on the migration abilities of the species and the presence of migration barriers. Therefore, it requires information on (i) the location of source populations, (ii) the species’ dispersal abilities, (iii) the spatially explicit technical implementation of dispersal modelling (e.g. as a GIS model), and optionally, (iv) the location of migration barriers.

For fish dispersal, existing models mainly covered conceptual frameworks (e.g. McMahon and Matter 2006), complex mathematical or theoretical formulations (e.g. Ovaskainen 2008), or empirically derived movement patterns (e.g. Radinger and Wolter 2013, Rodríguez 2002), while a model to predict the spatially explicit dispersal was missing. The fish dispersal model FIDIMO developed for the modelling framework by Radinger et al. (2013) provides such a novel software module to predict fish movement in a spatially explicit river network in the free and open source GRASS GIS (Neteler and Mitasova 2007). The river network is rasterized and the dispersal of fish is modelled starting from each spatially explicit source population. The probability of fish moving from the sources to other raster grid cells is calculated using a leptokurtic diffusion kernel consisting of two superimposed normal distributions. The equation describing the diffusion kernel function is parameterized using statistical regression models that are based on a meta-analysis of empirical studies on fish movement (mark-recapture studies) and include the following parameters: fish length, aspect ratio of the caudal fin, stream order, and time (Radinger and Wolter 2013).

The main input for FIDIMO is a (raster) map of the river network containing locations of source populations, the parameterization for the leptokurtic diffusion kernel, and optionally the location and characteristics of migration barriers. The location of source populations can be (i) either based on sampling data – probably underestimating the number of sources since only a limited number of locations can be sampled, (ii) or predicted using species distribution models using explanatory variables as proxies for the presence of species and source populations – probably overestimating the number of sources where the habitat is suitable but other pressures are constraining colonization. The output of FIDIMO is a map indicating the probability of occurrence in the raster cells of the river network (Radinger et al. 2013).
For *invertebrate dispersal*, empirical data on the movement distances and migration abilities are scarce, and information are mainly restricted to gross classifications of dispersal abilities (Poff et al. 2006). Furthermore, the dispersal of merolimnic invertebrates fundamentally differs from aquatic fish and invertebrate fauna due to the terrestrial life-stage, and the dispersal distances largely depend on the dispersal mode (aquatic dispersal vs. terrestrial dispersal), with aquatic and terrestrial landscape features both influencing the species-specific dispersal patterns. In contrast to diffusion kernel functions, least-cost modelling is better suited to account for differences in the permeability of the landscape. It identifies the lowest accumulated (friction) cost between any raster cell and the source raster cells (source populations) (Adriaensen et al. 2003, Dedecker et al. 2007). Friction costs for aquatic and terrestrial landscape features are assigned based on literature data and expert judgment.

Least-cost models are widely applied in ecology, e.g. for terrestrial vertebrates (Adriaensen et al. 2003) and invertebrates (Koch and Smith 2008), as well as for aquatic organisms (Dedecker et al. 2007, Keller and Holderegger 2013, Sondermann et al. 2014). Respective tools are available in many GIS like r.cost in GRASS GIS or Cost Distance and Path Distance in ArcGIS (ESRI 2011). Least-cost modelling requires information on the location of source populations and the species-specific friction costs of landscape features, which have to be defined and modelled separately for the three dispersal modes of invertebrates: aerial dispersal (adult), aquatic upstream dispersal (larval), and aquatic downstream dispersal (larval). After calculating the lowest accumulated cost for all raster cells and each dispersal mode, a threshold value is used to classify raster cells as being reachable or not. The three resulting binary maps are then combined to give the number of dispersal modes by which each raster grid cell can be reached.

To **finally assess the effect of the different pressures on biota**, information on habitat suitability, water quality and physico-chemical aspects (e.g. nutrient loads), and the species pool available for (re-) colonization are combined.

Water quality and physico-chemical aspects can be considered by developing dose-response relationships or identifying thresholds based on empirical data. For invertebrates, the abundance predicted by the habitat model (HET) is corrected (reduced) according to the dose-response relationship between water quality parameters and species abundance (Kiesel et al. 2014, Guse et al. in prep.). For fish, the habitat suitability model does not predict species’ presence or abundance but gives values for the WUA, and hence, cannot be directly linked with dose-response relationships between water quality parameters and species abundance or thresholds for species’ presence. However, the effect of habitat suitability and water quality aspects can be compared descriptively.

Although developing dispersal models for fish (Radinger et al. 2013) and invertebrates (section 3.7) was a major step forward, dispersal modelling in rivers is still in its infancy. Presently, some parameters are not considered in the models (e.g. abundance of the source populations, reproduction), and hence, the probability of occurrence given by the models cannot be transferred into absolute numbers of individuals, which would be necessary to assess if populations can establish. However, species can be ranked according to their relative (re-) colonization potential. In combination with a ranking according to the habitat suitability, species can be classified as having a high or low probability to establish in the study reach (high or low habitat suitability) in the short or long term (high or low (re-) colonization potential) (**Fig. 3**).

In addition to assessing the effect of pressures for the specific location of the study reach, the general potential effect of restoring reach scale habitat conditions at the river network scale can be
considered by quantifying the share of the river network which can be reached, i.e. the (re-) colonization potential of the whole river network. This allows to assess the effect of restoring reaches in the river network to similar habitat conditions found in the near-natural study reach given the conditions at larger spatial scales like the (re-) colonization potential.

In a feedback loop, interaction models can be used to assess the influence of biota on water quality, flow and substrate conditions as well as other environmental variables. In the IMPACT project, the feedback of biota on water quality parameters has been investigated in one of the study catchments, but in principle any other “ecosystem engineering” effect can be considered in the modelling framework given that respective models are available or will be developed.

The output of ecohydrological models are time-series of the modelled parameters, usually with a daily resolution, which cannot be directly used in the following modelling steps since it is neither feasible nor useful to predict the morphological changes, habitat conditions and suitability with such a high temporal resolution. Therefore, it is necessary and crucial to extract morphologically and ecologically meaningful hydrological variables describing the flow regime.

In the morphological models used, formative discharge is a necessary input, i.e. a single discharge value which determines sediment transport and channel morphology. Effective discharge is often selected as formative channel-forming flow, which is the discharge transporting most sediment in respect to the magnitude and frequency. In gravel bed rivers, effective discharge often corresponds to bankfull flow (1-2 y recurrence interval, see review in Soar and Thorne 2001). In sand bed rivers, effective discharge is more variable (Soar and Thorne 2001, Crowder and Knapp 2005), usually less than the 1.1 year flood event (Crowder and Knapp 2005), but still strongly correlated to bankfull discharge (Soar and Thorne 2001, Xu, 2004). However, bankfull discharge by definition depends on channel cross-section form and is not a flow regime variable which can be derived directly from the hydrograph predicted by the ecohydrological model. Therefore, it is necessary to select a flow regime variable as proxy first, which is related best to bankfull discharge.

In ecological literature, magnitude, frequency, timing, duration, and flashiness are usually listed as ecologically meaningful flow regime variables, and, besides mean values, high/low flow events are considered important since they often serve as ecological bottlenecks (Richter et al. 1996, Poff et al. 1997). The magnitude and frequency of extreme events can be considered by selecting discharges with a high and low probability of occurrence, respectively. Mean low and high flow values calculated based on an annual maximum and minimum series can be used (Hauer et al. 2012). Alternatively, a higher temporal resolution can be considered by selecting the upper and
lower quantile of daily values, i.e. the flow exceeded 25% and 75% of the days (high flow Q25 and low flow Q75) (Richter et al. 1996). Furthermore, more extreme events like the absolute minimum or maximum flow are important flow regime variables but there are practical limitations of using them in the integrated modelling framework since (i) local instabilities and artefacts tend to occur in 2D hydrodynamic models at very low discharges, (ii) they represent rather stochastic events with a high measuring and modelling uncertainty. Timing can be considered by distinguishing between different time periods, e.g. calculating mean seasonal or monthly values (Richter et al. 1996). In the IMPACT project, three hydrological variables (Q25, Q50, Q75) were calculated based on the modelled hydrograph to describe the flow regime and used in the subsequent modelling steps. For specific research questions it might be more appropriate to use other flow regime variables or time-periods, e.g. the spawning life stages instead of monthly values to assess habitat suitability for specific fish species (Escobar-Arias and Pasternack 2010).
2.2 STUDY CATCHMENTS AND STUDY REACHES

The three case-study catchments are located in Northern Germany (Treene), south-western France (Célé), and south Portugal (Quarteira).

The Treene River is a mid-sized (481 km² non-tidal influenced), naturally heavily meandering, lowland sand-bed river with gravel patches (Pottgiesser and Sommerhäuser 2008). Presently, large parts of the river network are in a moderate to poor hydromorphological state according to the standard assessment method (LAWA 2000), and catchment land-use is dominated by intensive agriculture (80%). The near-natural study reach 260 m in length is located in the lower part of the catchment (227.0 km²), freely meandering and bordered by grassland (54°35’2.65”N, 9°20’22.10”E). Mean discharge is 3.0 m³/s, bankfull discharge 6.0 m³/s, mean bankfull width and depth 10.9 m and 1.4 m, slope 0.45‰, bed-material is pure sand (D₅₀ = 0.16 mm), bank material is cohesive (80-100% silt/clay content), and uniform discharge can be assumed since no tributary is entering along the reach.

The Célé River is a mid-sized (1,346 km²) river consisting of two different sections. The upper and middle course are naturally wandering to meandering with gravel bed material. The lower reaches are located in the Célé River gorge, i.e. the river is flowing through a deeply incised valley with substantial parts of the bed consisting of bedrock outcrops. In the middle course, most of the banks are fixed and reaches are entrenched and bordered by agricultural land use, except for the study reach, which is located about 8.0 km downstream of Figéac (44° 35’ 21” N, 01° 57’ 29” E, 761.3 km²), where natural channel dynamics caused lateral erosion and the formation of natural channel features. This near-natural study reach is 260 m in length, mean discharge is 5.9 m³/s, slope is 1.76‰, bed material consists of poorly sorted medium to very coarse gravel (D₅₀ = 34 mm), and bank material consists of gravel overlain by cohesive material.

The Quarteira river is a mid-sized (325 km²) boulder to gravel-bed, naturally probably wandering river, which is located in the Algarve region (Portugal) and drains to the Mediterranean Sea. Mean annual precipitation is 625 mm/a, with high precipitation in winter and a dry summer. Due to the low precipitation in summer and the karstic geology, the Quarteira river is intermittent and dry during most of the summer. The landscape is characterised by a mosaic of olive trees, vineyards, orchards and a mixtures of forests. The downstream part is heavily degraded and near-natural reaches are only found in the upper parts of the catchment. The most downstream near-natural reach was selected for this study (37° 11’ 18” N, 08° 05’ 27” W), which is 290 m in length, has a slope of 3.79‰, and is located in a tributary (Algibre river).

During the field campaigns, channel bathymetry, flow, and substrate of the near-natural reaches were mapped, and biological samples were taken. Mapping at the Treene River was done in March 2011 during mean flow conditions, which allowed meaningful flow measurements, based on which e.g. roughness values can be back-calculated. The study reach in the Célé was mapped in September 2011 at exceptionally high discharges for the time of the year, which allowed to take meaningful flow measurements. Invertebrate samples at the Célé were already taken in June 2011 since the larvae of many species emerge in early summer and hence, cannot be adequately sampled in late summer. Data were used to set up and calibrate the 2D hydrodynamic and habitat models.

The field campaign at the Quarteira had to be postponed from winter 2011/2012 to January 2013 since the river was dry even in winter due to exceptionally low precipitation. The pressure loggers
installed in winter 2012/2013 got stolen in spring 2013 just prior to the summer dry period. Therefore, no data were available to develop a rating curve, which would have been necessary to set up and calibrate the 2D hydrodynamic model. Due to these unfortunate circumstances, it was not possible to model the hydraulic habitat conditions and habitat suitability at the Quarteira. The available person month were used to model the land use changes at the Treene River in more detail, which was indicated by the local river managers being a highly relevant issue.
2.3 MODEL SETUP AND CALIBRATION

In the following, setup and calibration of the models for which software applications were already available will be briefly described. This background information is given to ease interpretation of the results. The two models which have been developed in the IMPACT project will be described in more detail (fish dispersal model, invertebrate habitat evaluation tool).

2.3.1 SETUP AND CALIBRATION OF EXISTING SOFTWARE APPLICATIONS

**Ecohydrological model (CAU):** The hydrological modelling was carried out with the eco-hydrological model SWAT (Soil and Water Assessment Tool, Arnold et al., 1998; Arnold and Fohrer, 2005). The SWAT model is a continuous catchment model which is structured in localized subbasins and non-localized hydrological response units which have the same characteristics like land use, soil and slope. SWAT models were set up and calibrated to measured discharge data in all three catchments, using six hydrological stations in the Treene catchment, while data of only two (Célé) and one (Quarteira) stations was available in the other two catchments. Nevertheless, model performance was satisfying in the Célé catchment (Nash-Sutcliffe efficiency index of 0.56 for calibration and 0.59 for validation, and good in the Treene catchment (0.65 to 0.82 in the calibration and 0.58 to 0.80 in the validation period). Similar to discharge, long time-series are needed to model water quality, which usually are not available. However, in the Treene catchment, a two-years measurement campaign for sediment, total phosphorus and nitrate in the IMPACT project allowed to set up and calibrate water quality models. The SWAT model results show a satisfying performance in terms of the Nash-Sutcliffe Efficiency Index for nitrate (0.62 in the calibration, 0.74 in the validation) and for total phosphorus (0.56 and 0.37), while the performance of the modelled sediment was less (0.46 and 0.10).

**1D hydrodynamic model (CAU, IGB):** The water level at the downstream end of the study reach is needed besides discharge to run the 2D hydrodynamic model. For the Treene study reach, a respective rating curve was developed based on a 1D hydrodynamic model. A HEC-RAS model was set-up for a three kilometre long river segment in the Treene River ranging from the study site to the next hydrological station located downstream. Forty-two cross-sections and flow-velocity were mapped in this segment in June 2011, and used to develop a rating curve for the study reach based on the records of the hydrological station. Due to the spatial proximity of the gauging station in Figéac, the rating curve for the Célé study reach was developed based on gauging data. Water levels at the downstream end of the study reach were measured 01/13-05/13 using a pressure sensor. The corresponding discharge was assessed by multiplying the gauging data with the ratio of study reach and gauging station catchment sizes. The resulting rating curve showed a good fit ($r^2 = 0.96$).

**Morphological models (IGB, UU, IHE):** The study reach is one of the most natural sections of the Célé River where natural morphodynamics formed natural instream channel features like pools, riffles, and bars. However, bankfull channel geometry was not yet well developed, and the reach has only been freely migrating for about the last 20 years, which is not sufficient to calibrate morphological models. In contrast, the study reach in the Treene River has been freely meandering for decades and aerial photographs on channel planform were available from 1953 on, which allowed setting up and calibrating models for bankfull channel geometry and channel planform.
Channel geometry: For the Treene River, an empirical hydraulic geometry equation was developed, and an existing regime model for gravel bed rivers was adapted to sand-bed rivers with cohesive banks. To develop an empirical equation for channel width of the Treene River, 14 comparable near-natural river reaches in northern Germany were mapped. Bankfull channel width \((W)\) was strongly related to bankfull discharge \((Q_b)\) at the river reaches mapped \((p <0.001\, , \, r^2 = 0.81, \, n = 13)\), and a power function \((W = 6.19 \, Q_b^{0.33})\) showed a better fit compared to a simple linear relationship. The lower slope of the regression line compared to other empirical equations for sand-bed rivers (Soare and Thorne, 2001, Xu, 2004) is probably due to the increase of silt/clay content, and hence bank stability with river size, and hence discharge. Moreover, other regime equations were developed based on data from much larger rivers \((W >> 10 \, m, \, Q_b >> 10 \, m^3/s)\) and in other regions. In contrast to the present bankfull discharge, the future \(Q_b\) is not known and cannot be predicted since it depends on channel geometry, which in turn is the dependent variable to be modelled. However, future hydrological characteristics like flows with a specific recurrence interval (based on an annual maximum series) or a specific probability of exceedance (based on flow duration curves) can be predicted based on the hydrograph of the catchment model. Based on gauging data, \(Q_{39\text{d}}\) (flow exceeded 39 days per year, i.e. about 10% of the days, \(Q_{10}\)) was identified as the best proxy for bankfull discharge. In the corresponding power function \(W = 6.69 \times Q_{10}^{0.28}\), \(Q_{10}\) was even more strongly related to bankfull channel width \((r = 0.91)\) compared to \(Q_b\) itself.

Bank stability strongly influences bankfull channel width besides bankfull discharge. However, since silt/clay content was co-correlated with bankfull discharge in the sand-bed rivers investigated, it was not possible to quantify the effect of bank material on stable channel width of the Treene River using an empirical hydraulic geometry equation. As an alternative, an existing regime-model for gravel bed rivers was adapted for sand-bed rivers with cohesive banks. The regime model was based on the model of Millar and Quick (1993), modified by Eaton and Millar (2004), and available as an Excel Solver version called UBCRM (University of British Columbia Regime Model) at the website of Brett Eaton: http://www.geog.ubc.ca/~beaton/UBC%20Regime%20Model.html. For a detailed description of the regime equation and regime model please see the mid-term report.

Channel planform: The MIANDRAS model (Crosato 2008) was selected to predict planform changes and dynamics, since it considers both migration processes (fluvial entrainment and mass failure), is capable to reproduce stationary bars, and has already been successfully applied in several field studies (Crosato 2008). For model calibration, channel width was measured in the field, channel roughness was back-calculated from measured flow velocity data, grain size was determined from dry sieving of bulk samples, and a time-series of aerial photos (1953-2008) was used to derive empirical data on past channel migration rates. Bankfull discharge was assessed considering the whole study reach instead of only using data on single cross-sections, as recommended by Navratil et al. (2006). The 2D hydrodynamic model of the study reach was used to calculate the wetted area for different discharges. Bankfull corresponds to the discharge above which the wetted area sharply increases since the flow overtops the banks and inundates the large floodplain areas. The 2D modelling results indicated that this occurs at about 6.0-6.5 m³/s, which corresponds well with the \(Q_{10}\) of 6.57 m³/s predicted by the ecohydrological model (with \(Q_{10}\) being the flow regime variable which was identified as the best proxy for bankfull discharge).

Channel bathymetry: The 2D morphodynamic model of the Treene study reach was set up and calibrated by the Dutch subcontractor at the University of Utrecht (Filip Schuurman from UU). The UU also modelled the equilibrium channel bathymetry based on the \(Q_{10}\) (proxy for bankfull
discharge) predicted by the ecohydrological model for the baseline scenario, i.e. present discharge conditions.

**2D hydrodynamic models (IGB):** The FaSTMECH solver of the iRIC software was used as 2D hydrodynamic model since computational time is low despite (i) the large number of planned climate- and land-use scenario runs for monthly values of different flow regime variables, and (ii) the high resolution of the computational grid of about 0.2 m², which was chosen to model hydraulics at a spatial scale relevant for invertebrates. Moreover, it is freeware (http://i-ric.org/en/introduction).

For the Treene study reach, the best fit between mapped and modelled water levels (mean difference 6 mm, max. 15 mm) was obtained for the calibration discharge of 2.2 m³/s using a Manning n of 0.040 (initial roughness value back-calculated from measured flow velocities Manning n = 0.058). This can be considered a good fit given the mapping accuracy of 5 mm, the maximum error of discharge (1.7%) being well below the acceptable error of 3% given in the FaSTMECH manual, and since the observed flow patterns were reproduced. Morphodynamics and sediment sorting was not modelled for the Treene case-study since bed substrate was pure sand, except for the macrophytes at the river margins. The habitat model for invertebrates (Habitat Evaluation Tool, see below) predicts the presence and abundance of invertebrates on different substrates based on empirical substrate-specific sampling data. For the invertebrate sampling and habitat modelling, sandy substrate is subsumed in one single substrate class, and hence, any sediment transport and sorting of the sandy substrate would have no effect on the habitat modelling results. For macrophytes, there is no model available to predict macrophyte presence and abundance and the effect of discharge and nutrient load changes in the different climate and land use scenarios. Such a model is urgently needed since macrophytes potentially strongly affect channel hydraulics and morphology and, hence habitat conditions for macroinvertebrates and fish. However, developing such a model, which also should include the feedback of changed channel morphology on macrophytes, is a major task and was beyond the scope of this project.

For the Célé study reach two computational grids were used to increase model accuracy. In FaSTMECH a curvilinear orthogonal grid is used following the main flow direction. The Célé study reach is highly curved and very wide with a large bar and side channel, and as a result, the borders of the model grid cells intersect in the inner bend for computational grids with the high spatial resolution of 0.2 m used in this study. At higher discharges, the main flow direction is less curved and the computational grid can cover the whole width of the wide channel but modelling results are less precise for lower discharges.

For low to medium discharges up to 20 m³/s, a highly curved grid following the main flow direction was used, not covering parts of the inner bend and side channel, which are not wetted anyway at these flows. The best fit between mapped and modelled water levels (mean difference 7 mm, max. 11 mm) was obtained for the calibration discharge of 0.99 m³/s using the initial roughness value back-calculated from measured flow velocities (Manning n = 0.058). This can be considered a good fit given the mapping accuracy of 5 mm, the maximum error of discharge (0.8%) being well below the acceptable error of 3% given in the FaSTMECH manual, and since the observed flow patterns were reproduced.

For high discharges > 20 m³/s, a less curved grid was used which covers the whole river channel. For calibration, water levels and flow velocities predicted by the first model grid for Q = 20 m³/s were used. The mean difference of water levels (5 mm), discharge (0.8%), and flow velocities (0.045 m/s) indicate that the two models give comparable results. Since finally only 5 out of the 72
scenario runs had discharges larger than 20 m$^3$/s, the use of the two different computational grids potentially only had a small effect on the overall modelling results.

**Habitat model for fish (IGB):** The assessment of the suitability in the selected study reach at the Treene and Célé was conducted for single fish species based on monthly discharge data and species specific habitat preferences to also cover seasonally varying suitabilities of the habitat. Due to the well-known opportunistic resources use and broad environmental tolerances of many species, one of the more recently developed fuzzy logic habitat suitability models was used, namely the GRASS GIS tool r.fuzzy.system (Jasiewicz, 2011) since it is a more general implementation of Zadeh’s (1965) and Mamdani and Assilian’s (1975) fuzzy inference system within a geographical information system for large datasets. Furthermore, r.fuzzy.system is entirely based on open source software, highly flexible and can accommodate any combination of custom input raster maps like imports from other software. The inputs required by r.fuzzy.system are (i) the raster maps with the predictor parameters, (ii) a MAP file that defines the fuzzy membership classes for the input (e.g. flow velocity and water depth) and output parameters (e.g. habitat suitability) and (iii) a RULE file that describes the relationship of all possible parameter combinations and the resulting species- and/or life stage-specific habitat suitability. The species-habitat relationships considering flow velocity and water depth (RULE file) were developed for all single fish species separately based on expert judgement. The modelling process which involves the pre-processing of the input maps (transformation from the 2D hyrodynamic model output to a GRASS raster map) and the core fuzzy modelling was programmed as automatized python scripts. This automatization allowed multiple model runs for many species and for different climate change and land use scenarios. In total, 26 respectively 29 fish species/lifestages were modeled and monthly values for WUA for all three hydrological percentiles as well as for all climate and land-use scenarios were calculated.

**Dispersal model for invertebrates (UDE):** For invertebrates, the knowledge on movement distances and dispersal abilities of most species is limited, information like mark-recapture studies for fish are missing and rather based on categorical assessment (e.g. high dispersal capacity, low dispersal capacity, Poff et al. 2006) as opposed to the analysis of empirical data. A review of the literature indicated, that dispersal distances of individual species are largely dependent on the dispersal mode (e.g. aquatic dispersal, terrestrial dispersal), with aquatic and terrestrial landscape features both influencing the species-specific dispersal patterns within a study area.

To account for these species-related differences we used a “least-cost” approach that has so far been applied for terrestrial vertebrates (Adriaensen et al. 2003) and invertebrates (Koch and Smith 2008), as well as for aquatic organisms (Dedecker et al. 2007, Keller & Holderegger 2013, Sondermann et al. 2014) within the scope of biological studies. The “least-cost” algorithm is used within the tools Cost Distance (ESRI 2011a) and Path Distance (ESRI 2011b), both implemented in the Spatial Analyst extension of ArcGIS 10.0 (ESRI Inc., Redlands, CA, USA). It identifies the lowest accumulated (friction) cost between any raster cell and the source raster cells, given in this study as the source populations of a species (Adriaensen et al. 2003, Dedecker et al. 2007). Friction costs for aquatic and terrestrial landscape features were assigned based on literature and expert judgment (for detailed information see Sondermann et al. 2014).

As an input for the model, we used a raster map of the species source populations similarly to the fish dispersal modelling approach (source populations were either taken from species distribution models or based on original sampling data, see section 2.3.2). Overall, the model was applied for three dispersal modes, comprising i) aerial dispersal (adult) ii) aquatic upstream dispersal (larval)
and iii) aquatic downstream dispersal (larval), neglecting catastrophic drift events and zoochorie. It is well known, that the movement of most individuals of a distinct source population is confined to a small extent, whereas some individuals from the same population are able to disperse over long distances. To account for this fact, we both included a conservative dispersal approach (assuming low dispersal distances) and a progressive dispersal approach (assuming high dispersal distances).

For each species and dispersal mode “Friction cost maps” were generated based on the available source populations and the a priori defined set of friction costs. After applying the “least-cost” algorithm, the resulting “least-cost” maps were combined for each species. The output of the model is a raster map displaying the maximum dispersal extent of a species within one life cycle by the number of raster cells that can be reached by any of the three dispersal modes.

**Interaction model (CCMar):** Mediterranean intermittent type rivers are characterized by sequential events of flooding and drying, based on seasonal and annual weather patterns. Extreme hydrological conditions (very low and high flow) are considered to be a primary source of environmental variability that shapes the biological communities and their productivity. Primary production and respiration are direct and functional measures of the ecosystem. They provide information about the production and use of organic matter and therefore give insight about energy flow in the river trophic web. Since metabolism metrics include functional component of the ecosystem they provide more adequate response of aquatic biota to physical and chemical stressors than simple structural measures (i.e community composition measurements, Young et.al. 2008). Accordingly, this metric to analyze the metabolism of the three most common aquatic habitats in the Quarteira river (stones with algae, gravel and leaf litter) by measuring in situ, the respiration and photosynthesis rates, during two seasons (winter and summer). With this work we aim to understand the seasonal variability in this ecosystem metabolism, as a basis to predict future changes in water quality related with climate scenarios for the region. In the broader context of the IMAPCT project, data from these experiments will be used to parameterize the secondary functional feedbacks from biotic to abiotic controls on water quality and habitat conditions.

The study-reach was located in the Algibre stream (37°11'18"N, 8°05'27"W), a first order stream located in the Quarteira River Basin, which is characterized by intermittent discharge and strong seasonal variation in the occurrence of different substrate types (mesohabitats) (see section 2.2). The experiments were conducted during February and May (winter and summer), in parallel with geomorphological surveys leading to detailed habitat maps corresponding to each period. In winter, the most common habitats (accordingly to our geomorphological survey) were: ‘gravel’; ‘gravel in riffle’ (covered with thick layer of biofilm that was present only in gravel encountered in riffles), ‘stones with algae’ and ‘leaf litter’. During summer, we identified the same type of mesohabitats as in winter, except for ‘gravel in riffle’.

Changes in dissolved oxygen concentrations (mg l⁻¹ h⁻¹) were measured in situ, utilizing benthic chambers, where the undisturbed substrate with its biological community was enclosed in a transparent chamber filled with stream water. Respiration measurements were conducted after covering the chamber with a plastic cover to inhibit light. The incubation time was 1.5 h for each light/dark measurement. Gross Primary Production (GPP) was estimated as the difference between measurement in light and dark. One way ANOVA was used to detect differences in GPP and Respiration among habitats for each season. The results were further extrapolated to reach scale on the base of the habitat cover maps using ArcGis 10.1 software.
2.3.2 DEVELOPMENT OF NEW BIOLOGICAL MODELS

Habitat model for invertebrates (UDE): Conventional habitat models describe the relation of a selected species towards a certain habitat (composition) as a measure of probability of occurrence or as the amount of suitable habitat for a species within a study reach (see habitat models in section 2.1.). Consequently, most models do not predict any probability of species presence or even abundance. To overcome these limitations, we developed the Habitat Evaluation Tool (HET), a univariate, statistical-empirical habitat model that predicts the presence and abundance of invertebrate species within a certain river reach based on empirically derived relationships between habitats and species presence and abundance (Kiesel et al. 2014).

In general, the HET modelling approach consists of three consecutive steps: i) a generating dataset consisting of a larger number of habitat-specific samples is used to calculate the presence and mean abundance of species on specific habitats (e.g. sand, gravel, wood substrate, called Habitat Sensitivity Classes HSC) as well as the percentage of each species in each habitat (i.e. values of all species sum up to 100% for each habitat, e.g. substrate type), (ii) a large number of virtual “electronic” samples are taken from each habitat, with the number of individuals randomly drawn per habitat corresponding to the mean number found in this habitat in the empirical samples; these habitat-specific virtual samples are weighted according to the share of the habitats (e.g. coverage of different substrates) in the study reach, (iii) the resulting composite taxalists can be analysed using standard assessment methods (for more detailed information see Kiesel et al.

![Flow-chart of the Habitat Evaluation Tool (HET).](image)
as one of the most significant variables for explaining spatial distribution patterns of benthic invertebrates (Beisel et al. 1998) on a micro scale. Therefore, the HET was applied in the IMPACT project using substrates as Habitat Sensitivity Classes. Due to this, the model performance is constrained by nature and certainly limited by the temporal and spatial resolution of the selected variable (substrate), especially since macorinvertebrates establish complex relationships towards various environmental parameters. However, in principle, the modelling approach is not limited to substrates as Habitat Sensitivity Classes and any other (combination) of environmental variables can be used as far as a habitat-specific empirical sampling dataset (calibration dataset) is available.

The HET was scripted using the programming language python (Version 3.3.0) and can be easily implemented in the free and open source software CPython. Depending on data availability, the script can be adapted to perform not only univariate, but multivariate simulations as well (e.g. Substrate AND flow velocity). However, this data was not available within the scope of this study.

Dispersal model for fish (developed by IGB, complementary genetic approach by UPS):
Quantifying fish dispersal and identifying its general predictors is central to understanding many ecological processes and predicting population responses to environmental changes. Despite increasing efforts in river restoration and the needs for predicting re-colonisation of restored river habitats by fish, there has been no comprehensive and quantitative analysis of heterogeneous fish movement.

**Literature Study: Dispersal patterns and abilities of riverine fish**

Dispersal, defined as a one-way movement away from an animal’s site (Lidicker and Stenseth, 1992) arises from behavioural decisions on individual level in various life stages and at different temporal and spatial scales (Fausch et al., 2002). It acts as a key determinant in population dynamics and interactively links ecology, behaviour, genetics, and evolution (Lidicker and Stenseth, 1992; McMahon and Matter, 2006). It is recognized as a fundamental process taking place in stream networks along linear and branched dimensions (Fagan, 2002; Lowe and Likens, 2006). Despite knowing of its ecological importance for gene flow (Heggenes et al., 2006), spread of species and re-colonisation of newly available habitats (Albanese et al., 2009; Detenbeck et al., 1992), there is only sparse information on the spatial and temporal scales of fish movement. We lack general information on the quantities of dispersal and the share of mobile dispersal-relevant individuals, particularly with regard to a challenging future of changing environments involving climate change, habitat loss and fragmentation. (Kokko and Lopez-Sepulcre, 2006) as well as the need to restore rivers and to colonize the new habitats.

After some early attempts of measuring fish movement over various spatial and temporal scales (Thompson, 1933), the scientific field of fish movement became controversially discussed mainly pinned on the central question, of how mobile or resident fish are. The perceptions ranged from Gerking’s (1959) ‘restricted movement paradigm’ RMP (sensu Gowan et al. 1994) to considering fish as totally mobile populations (Linfield, 1985). Moreover, movement of vertebrates such as fish can be highly biased and underestimated due to field observations in finite study areas (Koenig and Vuren, 1996). In recent years, the concept of heterogeneous movement developed (Skalski and Gilliam, 2000; Rodríguez, 2002), which combines the two extreme views mentioned above, and considers fish populations consisting of both, a stationary and a mobile component.
When the distance moved by individual fish is plotted in a distribution function (distance moved vs. probability of occurrence, Fig. 6), the stationary component is reflected by a high peak of the leptokurtic dispersal kernel. In contrast, the mobile part of a population is characterized by a remarkably wider spread and higher ability to move and becomes apparent in a leptokurtic dispersal kernel as typical fat tails. Thus, the mobile component can be regarded as responsible for individual exchange between populations and is decisive for dispersal. Accordingly, the number of mobile individuals probably determines the successful colonization of new habitats and assessing their proportion might indicate the minimum size of a suitable founder population. A leptokurtic dispersal kernel can most accurately describe heterogeneous fish movement (Rodríguez, 2002; Skalski and Gilliam, 2000):

where $\sigma_{\text{stat}}$ represents the mean movement distance of the stationary component, $\sigma_{\text{mob}}$ represents the mean movement distance of the mobile component and $p$ is the share of the stationary component on the total population. The given dispersal kernel basically consists of two superimposed normal distributions and provides a probability of occurrence of an individual as a function of the distance ($x$) from the source population.

Based on empirical datasets from tables and figures from the literature, leptokurtic dispersal kernels were refitted and the three movement parameters ($\sigma_{\text{stat}}$, $\sigma_{\text{mob}}$, $p$) extracted. Besides the movement parameters, we also extracted information on potential explanatory variables for each dataset from literature. We hypothesized that these movement parameters strongly depend on (i) fish length, (ii) aspect ratio of the caudal fin, (iii) the size of the studied stream (discharge, stream width, stream order), and (iv) the duration of the study.

A total of 160 datasets were compiled from 71 studies. The studies were conducted in 16 countries spread over five continents and described the movement of 62 species from 12 families. As the largest groups salmonids, cyprinids, and centrarchids accounted for 56, 31, and 25 datasets and 12, 15, and 10 species, respectively. Three different sampling methods had been used in the studies, namely mark recapture (n = 119), telemetry (n = 31), and traps (n = 10). Total fish length ranged between 39 and 810 mm (median = 192.5 mm) and aspect ratio of the caudal fin ranged between 0.51 and 2.29 (median = 1.425).

The mean movement distance of the stationary component ($\sigma_{\text{stat}}$) ranged between 0.01 m and 39.76 km (median = 36.4 m), and the movement distance of the mobile component ($\sigma_{\text{mob}}$) ranged between 2.2 m and 166.4 km (median = 361.7 m). All explanatory variables extracted from literature (fish length (log $L$), aspect ratio of the caudal fin (AR), stream order ($SO^{1/2}$), discharge (log $D$), river width (log $W$) and time of the study (log $T$) were significantly positively related to the
distance moved by the stationary and mobile component \((\log(\sigma_{\text{stat}})\) and \(\log(\sigma_{\text{mob}}))\) (Pearson t-test, \(p < 0.005, n = 106 – 128\)). In contrast, there was no single significant predictor for the share of the stationary component \(p\) which ranged between 13.3% and 97.6% (median = 66.6%).

Fish length, aspect ratio of the caudal fin, stream order and time represent the best explanatory variables for \(\sigma_{\text{stat}}\) and \(\sigma_{\text{mob}}\) \((r^2 = 0.66\) and 0.78, respectively, \(p < 0.001, n = 96\):

\[
\log(\sigma_{\text{stat}}) = -10.57 + 1.64 \log(L) + 0.96 \text{AR} + 1.14 S0^2 + 0.43 \log(T) \quad (1)
\]

\[
\log(\sigma_{\text{mob}}) = -7.48 + 1.45 \log(L) + 0.58 \text{AR} + 1.51 S0^2 + 0.55 \log(T) \quad (2)
\]

On the basis of these empirically derived results, the dispersal abilities for single fishes can be predicted based on the species (fish length and aspect ratio), the river size and the time interval of interest. In addition, confidence intervals of the parameters can be calculated based on the empirical equations to consider the uncertainty in assessing the dispersal abilities in the dispersal model. A Software tool to parameterize the probability-density function based on these empirical relationships was programmed (R-package fishmove) and can be downloaded for free (http://cran.r-project.org/web/packages/fishmove/index.html). A detailed description of the dispersal abilities and patterns as well as the predictors is provided by Radinger and Wolter (2013).

**Identification of source populations**

The main input for a dispersal model is a map that contains locations of potential source populations as starting points for the dispersal process. Source populations can be determined either directly from empirical surveys using species occurrences (geographical locations of sampling sites) or indirectly from species distribution models (SDM) using preferred habitats as proxy for species presence and consequently potential source populations (Radinger et al., 2013). However, the first approach will most probably miss source populations due to false absence from insufficient spatial coverage of surveys, whilst the second approach tends to overestimate source populations, due to false presence from suitable habitat not colonised by the species.

For the Treene, SDMs were developed based on the statistical algorithm “Boosted Regression Trees” (BRT). BRT is a relatively new statistical method, which additively combines and averages (boosting) many simple regression trees. The resulting improved model typically shows high values of model quality (AUC) and typically performs well in variable selection and identification of interactions. BRTs can accommodate metric (continuous) but also categorical variables and the method is highly robust towards outliers or missing values. Furthermore BRTs do not require to transform the variables in advance as they do not assume a certain distribution of the variables (Death 2007).

**FIDIMO- Fish Dispersal Model for River Networks**

In the IMPACT project, FIDIMO (Fish Dispersal Model) has been developed to model fish movement and dispersal, based on open source GIS (Geographic Information System).

So far fish dispersal has mainly been discussed in conceptual models (McMahon und Matter 2006), complex mathematical models (Ovaskainen 2008) or theoretical formulae. These conceptual frameworks and equations can be used to describe and quantify riverine fish dispersal but comprehensive modelling tools to apply these equations in a specific river network and geographical setting, i.e. the implementation in a GIS fish dispersal modelling software were lacking (e.g. Bonhommeau et al., 2009; Wolter and Sukhodolov, 2008). Within the project IMPACT, FIDIMO, a first fish dispersal model for a GIS environment (add-on to the Open Source GIS
Software GRASS (Neteler und Mitasova 2007)) has been developed and is available for downloading (http://grasswiki.osgeo.org/wiki/AddOns/GRASS_6#r.fidimo).

The approach developed for fish is different from terrestrial dispersal in two ways: First, fish movement is restricted to the river corridor and this uni- or bidirectional dispersal is different from the radial terrestrial dispersal. Second, most individuals of a fish population are rather stationary and only few move longer distances.

The model has been developed to apply the characteristics of heterogeneous, species and size class specific fish movement on a rasterized river network including migration barriers. Fish dispersal is modelled as a leptokurtic diffusion process based on the empirically derived dispersal kernels (Fig. 5) spreading from spatially predefined source populations consisting of stationary and mobile components each. The probability distributions describe the movement of the stationary component and a smaller mobile component. Most current GIS software is basically able to model dispersal based on radial dispersal kernels. However, it is necessary to customize current GIS software tools to implement this leptokurtic approach on linear and branching elements such as rivers.

To run FIDIMO, the following input data are needed: the river network, locations of source populations, fish dispersal parameters defining the leptokurtic dispersal kernel and optional: locations and characteristics of movement barriers.

The size of the stream is considered in FIDIMO to account for the fact that the local stream size effects fish dispersal (see results of literature study above) and to model the upstream movement of fish at river junctions. In fact, the share of upstream moving fish which enter a tributary depends on the stream order of the tributary relative to that of the main stem. Besides stream size, the model results strongly depend on the presence and location of source populations, which can be provided either as random points or by user defined coordinate pairs. In either case, the most critical part is to predefine the exact location of the source populations.

As main results FIDIMO yields probabilities of occurrence of fish species in river raster cells based on empirically derived dispersal kernels after the time step of interest modelled. If information on the (relative) size of source populations is available (e.g. abundance, catch per unit effort) is available, this can be used to weigh the probability of dispersal accordingly. Consequently the probability does not only depend on the distance from the source population but also on its size. In addition, confidence intervals can be calculated to consider the uncertainty of the empirical relationships in assessing the dispersal abilities.

The final result of FIDIMO is a raster map providing probabilities of occurrence of fish species after a modelled dispersal step. Radinger et al. (2013) provide a detailed description of FIDIMO.

**Comparison GIS modelling vs. genetic approach**

This work was a close collaboration between the German partners (IGB) and the French partners (UPS). In addition to the application of the mechanistic fish dispersal model FIDIMO, dispersal was also modelled for selected species (e.g. Chub *Squalius cephalus*, European minnow *Phoxinus phoxinus*, Common dace *Leuciscus leuciscus*) using genetic modelling approaches (section 3.6.3). This allowed to compare the novel mechanistic GIS based dispersal model approach with another recent approach based on genetic markers.

First, a pairwise cross table (sample site matrix: sampling site x sampling site) was created including all sampling sites in the Célé which were also genetically analysed (n=12). This refers to the format that is commonly used for genetic similarity matrices. For each pair of sampling sites the
following parameters were calculated: Distance along the river network, number of migration barriers between the sites, passability of the single barriers and number of river confluences between the sites. Analogous to FIDIMO, the probability of reaching the other sampling site from the source site was calculated based on leptokurtic probability density functions (Fig. 6). Like for the raster based FIDIMO, this probability depends on the species-specific dispersal ability, the distance, the number and passability of barriers as well as on the number of river confluences. The model results provide a corrected species-specific probability how each sampling site can be approached from each other sampling site. Thus, the model runs also consider that each pair of sampling site can be analysed in up- and downstream direction, which, in sum, results in a joint asymmetric “mechanistic” dispersal matrix. Uni- and multivariate statistical regression analysis (matrix regression, MCMC (Markov Chain Monte Carlo) models) were used to compare the genetically with the mechanistically derived similarity matrices and to infer on the importance of single parameters like the quantification of the passability of barriers.

The main input for FIDIMO is a (raster) map of the river network containing locations of source populations, the parameterization for the leptokurtic diffusion kernel, and optionally the location and characteristics of migration barriers. The location of source populations can be (i) either based on sampling data – probably underestimating the number of sources since only a limited number of locations can be sampled, (ii) or predicted using species distribution models using explanatory variables as proxies for the presence of species and source populations – probably overestimating the number of sources where the habitat is suitable but other pressures are constraining colonization. The output of FIDIMO is a map indicating the probability of occurrence in the raster cells of the river network (Radinger et al. 2013).
2.4 SCENARIOS

(CAU)

In the following, the climate change and land use scenarios modelled in the Treene and Célé catchment will be described.

2.4.1 CLIMATE CHANGE SCENARIOS

For the Treene catchment, climate time series from the regional climate model STAR (Orlowsky et al., 2008) were used, which provide regionalized climate data with daily resolution for the whole of Germany based on statistical downscaling. In a resampling approach, the statistical relationships derived from measured temperature time series at climate stations from the past (from 1951 on) are used to predict future climate data until 2060. The STAR model includes 100 simulations which allowed to consider uncertainty in the climate scenarios. In the IMPACT project, the two most extreme STAR scenarios were used, the 0K scenario assuming no increase in temperature and the 3K scenario assuming a linear increase of temperature of up to 3K at the end of the modelling period (2021-2060). Four climate stations in and near the Treene catchment were used for the ecohydrological modelling.

For the Célé catchment, a reference scenario based on measured climate data (1961-2000) was compared to a climate change scenario (2021-2060) based on the A2 emission scenario of the IPCC. The A2 is one of the most pessimistic IPCC scenarios, and hence, its use can be considered a “worst-case” analysis similar to the use of the 3K scenario in the Treene catchment. Statistical downscaling of global climate change models of the A2 scenario was done for France in the DSCLIM project (régionalisation des scénarios climatiques par une méthode statistique par types de temps) and data were kindly provided by CERFACS (Centre Européen de Recherche et de Formation Avancée en Calcul Scientifique). Data on the recent climate conditions and climate change scenarios were available in the same raster format, and hence were spatially congruent and available area-wide for the whole Célé catchment with a resolution of 8 km.

2.4.2 LAND USE SCENARIOS IN THE TREENE CATCHMENT

Since the major recent changes of the land use in the Treene catchment were related to modifications in the agriculture crops, the focus of the scenario development was on the differences in the spatial and temporal distribution of agricultural crops rather than on changes of land use categories (e.g. conversion of grassland to cropland). An analysis of recent changes in the crops based on data from 2003 and 2010 illustrated a large increase in corn fields from 27% to 44% of the total agricultural areas. Thus, three different land use scenarios were developed (Geertz, 2012). Each scenario focused on different drivers of land use change. In the food scenario, an increase in food prices and hence, a higher share of wheat and corn was assumed (Fig. 7). In the energy scenario, a high demand for bio-energy and intensive research on alternative energy crops was assumed to result in an increase of alternative energy plants at the expense of corn fields. Similar changes were assumed in the best practise scenario which is focused on a structural diversity in the crop distribution. Here, the share of forages was assumed to get higher than in the energy scenario, while the rape share is lower. The share of the different
crops were not assumed being constant but to change dynamically from year to year over the modelling period. (2021-2030).

Fig. 7: Land use scenarios for the Treene catchment.
3 Results of scenario runs

In the following subsections, the results of the scenario runs will be presented: The climate change runs for the Treene and Célé River, and the land use scenarios of the Treene River.

3.1 ECOHYDROLOGICAL MODEL (CAU)

3.1.1 CLIMATE CHANGE SIMULATIONS IN THE TREENE CATCHMENT

The STAR 0K and 3K scenario data used for the Treene catchment consisted of 100 simulation runs, which were all used (i.e. modelled) for the modelling time period 2021-2060. The climate change simulations with the eco-hydrological SWAT model predicted a reduction in snowfall in winter and an increase in evapotranspiration due to a higher temperature, resulting in a reduction in percolation into soil and groundwater and lower groundwater recharge. Since discharge in the Treene river is dominated by groundwater, this also leads to a reduction of the total discharge.

The seasonal changes of precipitation and discharge were predicted to show a temporal shift. The effects of climate change on discharge have a delay of about two months compared to the effects on precipitation. A large decrease in rainfall was predicted in summer (June to August) and a small increase in winter. Correspondingly, the largest decrease in discharge was predicted in late summer and autumn (August to November) and a very small increase in winter. The two-month delay was related to the storage function of the catchment in soil and groundwater. The large decrease in discharge in late summer and autumn was predicted for all three hydrological variables.

Fig. 8: Modelled mean monthly discharge for the baseline (0K) and climate change scenario (3K) at the station Sollerup for different hydrological variables (Q75, Q50, Q25).
which were used to describe the hydrological regime (i.e. Q75, Q50, Q25, Fig. 8, detailed results on Q changes are given in section 3.3.1).

In addition to discharge, the effect of climate change on water quality parameters were modelled in the Treene catchment. For nitrate, mean monthly values showed a clear seasonal pattern with higher concentrations in winter and spring, and a significant decrease in the climate change scenario in all month. As a consequence, the number of days per month above a critical threshold for invertebrates of 5 mg/l decreases by about 50%. However, the critical threshold was predicted to be still exceeded in the climate change scenario in all month at least on some days. The effect of climate change and land use change is presented in more detail in section 3.1.3.

3.1.2 Climate Change Simulations in the Célé catchment

In contrast to the high number of model runs for the STAR climate data in the Treene catchment, one single model run was available for each scenario in the Célé catchment (and hence results were based on single mean values). Similar to the Treene catchment, the models predicted a decrease in snow fall and an increase in evapotranspiration due to a higher temperature, resulting in reduction of the total discharge. However, in contrast to the Treene catchment, the largest decrease in discharge was predicted in winter. Similar to the Treene, the decrease in discharge was predicted for all three hydrological variables which were used to describe the hydrological regime (i.e. Q75, Q50, Q25), but differences in winter month (December to March) were especially high for the low flow conditions (Q75), compared to the median and high flows (Q50, Q25, more detailed results on discharge changes are given in section 3.3.2).
3.1.3 LAND USE CHANGE SIMULATIONS IN THE TREENE CATCHMENT

The different land use scenarios had a small effect on discharge conditions compared to the climate change scenario (for more detailed results on discharge see section 3.3.1) (Fig. 10). Only, in autumn, a small increase in discharge was observed in the food scenario.

In contrast, the land use scenarios markedly affected water quality parameters, especially nitrate (Fig. 10, Guse et al., in prep.). Overall, nitrate concentrations were predicted to slightly increase in the food scenario but to markedly decrease in the energy and best practice scenarios as well as in the climate change scenario. Moreover, changes in nitrate concentrations showed a clear seasonal pattern.

Fig. 10: Difference of discharge and nitrate between baseline and climate change / land use scenarios (modelling period 2012-2030, Guse et al. in prep.).
3.2 MORPHOLOGICAL MODELS

The morphological models have been added to the modelling framework (i) to assess if the mapped morphological conditions are in equilibrium with the governing controls like discharge or if modelled equilibrium conditions should be used in subsequent modelling steps, and (ii) to assess the effect of discharge changes in the climate change and land use scenarios on channel morphology (see section 2.1.). Both aspects are addressed in the following subsections on channel geometry, planform, and bathymetry.

For the climate change scenario at the Treene River, median values of the 100 STAR runs have been calculated for the baseline (0K) and climate change (3K) scenario, and the modelling period (2020-2060) was divided into four 10-year periods by CAU. The morphological modelling was mainly done for the last 10-year period (2051-2060), where the largest discharge changes (Q10) were predicted by the ecohydrological model (Fig. 11), and hence, the results describe the “worst-case” conditions which occur during the modelling period. If no significant morphological change is predicted for this period, the same can be assumed for lower discharge changes occurring in other climate change scenario periods or land use scenarios.

3.2.1 CHANNEL GEOMETRY

The width predicted by the regime equation (11.2 m, 9.6-13.5 m 90% confidence interval) for the present Q10 (6.4 m$^3$/s) was similar to the mapped bankfull width of 10.9 m, indicating that channel geometry was near its dynamic equilibrium state.

Based on the general trend predicted for Northern Germany with small changes in total precipitation and an increase of extreme events, it was assumed that the frequency of flood events, and hence Q10 will increase. However, in the specific case of the Treene catchment, a significant decrease of 9.1% was predicted at the end of the modelling period (2051-2060) from 6.57 m$^3$/s to 5.97 m$^3$/s (Guse unpublished, Fig. 11). A 9.1% decrease of discharge corresponded to a decrease...
of bankfull channel width from 10.9 m (9.2 m - 12.8 m) to 10.6 m (9.0 m-12.4 m) according to the regime equation developed for sand bed rivers in Northern Germany, which was well within the 90% confidence interval given in parentheses. The regime model predicted a slightly larger decrease of bankfull channel width from 10.9 m to 10.0 m. A similar decrease resulted in the regime model from increasing bank stability (effective cohesion) from 5.05 kPa to 5.38 kPa, and the present channel width could be restored by a decrease to 4.75 kPa. These values for effective cohesion were well within the range of mid-sized rivers (bankfull depth 1-3 m) with grassy vegetation comparable to the Treene River (Darby 2005). These modelling results indicated that discharge changes caused by climate change will have no significant effect on bankfull channel width and local changes of riparian vegetation and bank stability potentially are more important in shaping channel-geometry at the Treene River.

3.2.2 CHANNEL PLANFORM

(IGB, IHE)

The empirical results on the past channel migration rates indicated that the Treene River had developed a natural freely meandering planform but was slowly migrating. The empirical migration rate of 6.6 cm/y, quantified using air photographs (1953-2008) was similar to the migration rate of 5.1 cm/y predicted by the empirical model of Julian and Torres (2006) for comparable conditions with a high silt/clay content of the river banks (~90%) and grassy vegetation. However the empirical and modelled migration rates were low. Obvious reason were (i) the dense grassy vegetation stabilizing the river banks along the whole river reach and a substantial part of river bank height, (ii) the cohesive bank material, (iii) the resulting low width/depth ratio, which hindered the formation of free alternate bars and resulting bank erosion, (iv) the formation of a second secondary flow cell generally establishing in very sharp meander bends which protects the outer bend from fluvial erosion (Lagasse et al. 2004). Besides the empirical data, the meander migration model was used to predict the long-term evolution of channel planform and the resulting equilibrium state. However, the Treene River study reach was a highly damped system due to the very stable banks and small width/depth ratio, meaning that any disturbance of the flow which induces the formation of bars and meanders rapidly diminishes downstream. The fact that the study reach was heavily meandering indicated that meander formation has occurred under different conditions (e.g. lower bank stability due to less dense riparian vegetation, frequent disturbance of the flow by large amounts of wood). This has important implications for river restoration in such rivers since restoring natural channel dynamics in a straightened reach will only result in meander formation if sparse riparian vegetation and/or the input of large amounts of wood is restored.

The discharge changes due to climate change were predicted to result in insignificant changes of channel planform dynamics (Fig. 12). Meander migration was predicted over the four 10-year periods in three different model runs starting from the present channel centreline for (i) the bankfull discharges (Q10) of the baseline scenario, (ii) the bankfull discharges of the climate change scenario, and (iii) in addition adapting the bankfull channel width according to the changed bankfull discharges. The mean migration rate of the channel centreline with 293 nodes was significantly lower for the third model run compared to the baseline scenario (paired t-test, p < 0.01, n = 293) but differences were negligible (1 mm decrease from 5.6 to 5.5 cm/y).
These modelling results indicated that medium-term discharge changes at the Treene river caused by climate change will have no detectable effect on channel planform and dynamics. Since discharge changes in the land use scenarios were even lower (see section 3.3.1), no morphological changes were to be expected in these scenarios. However, the results on the Treene River case-study do not imply that the morphological models can be neglected. Significant changes of channel morphology and habitat conditions can be expected in rivers with less stable banks, larger changes of bankfull discharge or riparian vegetation.

3.2.3 CHANNEL BATHYMETRY

(UU, IGB)

The equilibrium bathymetry markedly differed from the mapped bathymetry (Fig. 13); mean bed level was 14.1 cm higher, a deep pool in the upstream part of the study reach was largely filled, and cross-sections were more asymmetric and had higher maximum depth. The differences indicated that the mapped bathymetry might have been in disequilibrium and not representative of the channel bathymetry and habitat conditions. However, during additional field campaigns after mapping bathymetry in March 2011, visual inspection showed no major changes in channel bathymetry. Possibly, the differences were partly due to local instabilities causing modelling artefacts in some of the outer bends, and, although they were excluded from the analysis, might have affected the depth of nearby model grid cells. It appeared most likely that the differences are due to processes which were not covered by the 2D morphodynamic model like the effect of macrophytes on channel bathymetry and its feedback on macrophyte growth. Presently, there are first approaches to include aquatic vegetation in morphodynamic models (e.g. Schuurman, unpublished) but there is still a lack of knowledge on the ecology and hydraulics of aquatic vegetation. Since such extensive research was beyond the scope of the IMPACT project, the mapped bathymetry was used for the subsequent modelling steps.
Fig. 13: Comparison of channel bathymetry mapped in the field and modelled equilibrium state.
3.3 2D HYDRODYNAMIC MODELS

(IGB)

3.3.1 TREENE STUDY REACH

For the climate change scenario, the 2D hydrodynamic modelling focused on the last 10-year period (2051-2060), where the largest discharge changes were predicted by the ecohydrological model, and hence, the results describe the “worst-case” conditions which occur during the modelling period. If no significant morphological change is predicted for this period, the same can be assumed for lower discharge changes occurring in other climate change scenario periods. Moreover, the first 10-year period was considered to compare discharge changes caused by climate change to the results of the land use scenarios which were modelled for the same period (20121-2030). For both modelling periods, a total of 72 runs were modelled: 3 hydrological variables x 12 month x 2 climate change scenarios (baseline 0K and climate change 3K).

In the modelling period 2051-2060, the modelled hydraulic habitat conditions reflected the discharge changes predicted by the ecohydrological model, with all three hydrological variables Q25, Q50, and Q75 showing the same seasonal pattern (Fig. 16). In winter to early summer (January – June), the hydraulic habitat conditions were similar in the baseline and climate change scenario (Fig. 14, Fig. 15). In addition, habitat diversity was similar, which was reflected by the similar range of values of the 2D hydrodynamic model grid cells for flow velocity, flow depth, and shear stress (see boxes in box-plots Fig. 14, Fig. 15). Moreover, the mean value for all model grid cells only slightly differed between the baseline and climate change scenarios (mean percentage change over all three hydrological variables and 12 month for flow velocity 3.0%, flow depth 3.2%, shear stress 5.8%). In summer to autumn (July – December), differences were significantly higher (Mann-Whitney U test, p < 0.01, n = 36) and all hydraulic variables markedly decreased (mean percentage change over all three hydrological variables and 6 month for flow velocity -20.6%, flow depth -18.6%, shear stress -34.7%), especially during low flow (Q75) in October, for which the 2D hydrodynamic model predicted a decrease of the mean flow velocity and shear stress of the model grid cells by -44.0% and -68.6%, respectively (Fig. 16).

The results on shear stress indicated that critical shear stress of the bed material ($D_{50}$) was exceeded on large parts of the channel bed even in the climate change scenario where discharge and shear stress markedly decreased in late summer and autumn. It was only during low flow in autumn (Q75 in September and October) that a substantial part of the sandy channel bed was predicted being stable. This is of importance for macroinvertebrates since shifting sand are a hostile environment compared to stable sand. However, invertebrate assemblages on shifting and stable sand did not differ in the empirical sampling site data of UDE. Possibly, this is simply a methodological problem since substrate stability is usually determined in the field for the arbitrary, non-standardized discharge occurring during sampling at low to medium flow conditions. Alternatively, substrate stability could be determined for the discharges occurring over longer time periods (e.g. hydrograph throughout the year) using 1D or 2D hydrodynamic models. It was beyond the scope of the IMPACT project to set up hydrodynamic models for a large number of sampling sites but such models will be used to investigate the flow preferences of invertebrates in a recent project at the IGB. These results can be used to assess the effect of shear stress and substrate stability on invertebrates in the Habitat Evaluation Tool (section 2.1).
Fig. 14: Flow depth and velocity for the baseline (0K) and climate change (3K) scenario for 2051-2060 in the Treene study reach.
Fig. 15: Shear stress for the baseline (0K) and climate change (3K) scenario for 2051-2060 in the Treene study reach.
In general, the hydraulic habitat conditions reflect decrease in discharge but they cannot be directly deduced from the hydrological conditions. The percentage change of all three hydrological variables was significantly lower compared to discharge changes (Mann-Whitney U test, $p < 0.01$, $n = 36$). Moreover, the hydraulic variables did not decrease proportional to discharge. For example, the largest decrease at low flow conditions (Q75) occurred in November for discharge but in October for flow velocity and shear stress.

For the **modelling period 2021-2030**, the ecohydrological model predicted a significantly smaller change in discharge, with a mean change over all three hydrological variables and 12 month of 10.2% (Fig. 17) compared to 23.4% in 2051-2060 (Mann Whitney U test, $p < 0.01$, $n = 72$). Accordingly, the 2D hydrodynamic model predicted only minor changes of the hydraulic habitat conditions. In winter to early summer (December – June), the mean percentage change of the hydraulic variables was 2.4% and 7.5% at maximum. In summer and autumn (July – November) changes were significantly higher (Mann Whitney U test, $p < 0.01$, $n = 108$) but the predicted decrease was only about 1/3 compared to changes in summer and autumn 2051-2060 (mean percentage change over all three hydrological variables and 5 month for flow velocity -8.1%, flow depth -5.7%, shear stress -14.7%).
For the **land use scenarios**, a total of 288 runs were modelled: 3 hydrological variables x 12 month x 2 climate change scenarios x 4 land use scenarios (baseline, food, alternative energy crops - Energy, and best management). If only the pure land use effect is considered, i.e. the 144 runs for the climate change baseline scenario, the largest discharge changes occurred in the energy scenario, with a mean percentage change over all three hydrological variables and 12 month of 1.1% compared to 0.9% and 0.6% in the food and best management scenario.

As to be expected due to the small discharge changes, the differences of the hydraulic habitat conditions between the baseline and energy land use scenario were negligible (Fig. 18). In winter to early summer (December – June), the mean percentage change of the hydraulic variables was 0.5% and 4.7% at maximum. In summer and autumn (July – November) changes were significantly higher (Mann Whitney U test, $p < 0.01$, $n = 108$) but the predicted decrease was only about 1/5 and 1/20 compared to the changes due to climate changes in summer and autumn for the modelling period 2021-2030 and 2051-2060, respectively (mean percentage change over all three hydrological variables and 12 month for flow velocity -0.9%, flow depth -0.9%, shear stress -1.8%).

![Fig. 18: Percentage change of discharge and the hydraulic variables for the energy land use scenario (2021-2030) in the Treene study reach.](image)

In summary, it can be concluded that there will be negligible changes of the hydraulic habitat conditions due to the land use changes which were assumed in the three scenarios, and a minor decrease of flow velocity, depth, and shear stress in summer and autumn in the short-term (2021-2030) due to climate change. In contrast, the ecohydrological model predicted a major decrease of discharge, and the 2D hydrodynamic model a decrease of flow depth, and a major decrease of flow velocity and shear stress in summer and autumn in the medium-term (2051-2060).

The percentage change has been used to compare the hydrological and hydraulic variables which are measured in different units. At the low discharges in summer and autumn, a high percentage change corresponds to a rather low absolute change compared to the much higher discharges in winter. Moreover, the effect of these changes on biota depends on environmental-biological relationships, which often are non-linear or stair-stepped thresholds. Therefore, the modelled habitat conditions must be compared to the habitat needs of the species to assess possible effects on biota, which is done in section 3.4 and 3.5.
3.3.2 CÉLÉ STUDY REACH

Similar to the Treene study reach, a total of 72 runs were modelled: 3 hydrological variables x 12 month x 2 climate change scenarios (reference Re and climate change A2).

In general, the modelled hydraulic habitat conditions reflected the discharge changes predicted by the ecohydrological model, with a decrease of all three hydraulic variables in virtually all month (Fig. 19, Fig. 20). The decrease of discharge, flow velocity, and shear stress was significantly larger compared to the Treene study reach (mean value over all 3 hydrological variables and 12 month, Mann-Whitney U test, p < 0.01, n = 36). In contrast to the Treene study reach, (i) the largest decrease was predicted in winter (December – February/March) with a mean percentage change over all 3 hydrological variables of -31.8% (flow velocity), -17.3% (flow depth), and -50.8% (shear stress), and (ii) the seasonal pattern was less similar, especially in respect to the low flow conditions (Q75): In addition to the decrease in winter, an even stronger decrease was predicted for Q75 in summer (August, September), especially for flow velocity (-49.5%, -73.3%) and shear stress (-74.5%, -92.9%) (Fig. 21). Moreover, the percentage change of flow velocity ($F_{2/33} = 4.45$, $p = 0.020$) and shear stress ($F_{2/33} = 4.78$, $p = 0.015$) significantly differed between the three hydrological variables and was highest at low flow conditions Q75 (see Fig. 19 and Fig. 20 for absolute differences).

For shear stress in early winter (November, December), the 2D hydrodynamic model predicted an increase of the channel bed area where shear stress decreased in the climate change scenario and fell below critical shear stress of the bed material ($D_{50}$) even for relatively high flows (Q25) (Fig. 20). This indicated that sediment reworking, washing fine sediment downstream, will decrease prior to or at the start of the spawning season of salmonids. Moreover, the fully stable channel bed area at low flow conditions (Q75) increased in winter (December to February), indicating that the deposition of fines increases. These shear stress changes potentially impairs habitat conditions for winter spawner, and to a lesser extent spring spawner since the changes described above were less pronounced in March.
Fig. 19: Flow depth and velocity for the reference and climate change scenario in the Céle study reach.
Fig. 20: Shear stress for the reference and climate change scenario in the Célé study reach.
In summary, the 2D hydrodynamic model predicted a marked decrease of flow velocity and shear stress, especially in winter and during low flow periods. Moreover, an even larger percentage decrease was predicted for summer low flows (Q75 in August and September). Since absolute values were low during summer low flows, this large percentage decrease corresponds to a relatively small absolute change compared to the much higher discharges in winter. Therefore, the somewhat smaller relative changes in winter probably have a higher biological impact compared to the rather small absolute changes in summer. However, habitat suitability has to be modelled first to finally assess the effect on biota.
3.4 HABITAT MODEL FOR FISH

(IGB)

The assessment of the suitability of the hydraulic habitats of the study reaches at the Treene and Célé was modelled based on the results of the 2D hydrodynamic model (section 3.3) and the calculated flow velocities and water depths.

3.4.1 TREENE STUDY REACH

For the climate change scenario, the habitat suitability model is discussed separately for the period 2021-2030 and for the period 2051-2060. For the later 10-year period (2051-2060), the largest discharge and hydraulic changes were predicted by the ecohydrological model and the 2D hydrodynamic model, and hence, the results describe the “worst-case” conditions which occur during the modelling period. If no significant changes in the habitat suitability is predicted for this period, the same can be assumed for lower discharge changes occurring in other climate change scenario periods. Moreover, the first 10-year period was considered to compare habitat suitability changes caused by climate change to the results of the land use scenarios (section 3.1.3) which were modelled for the same period (2021-2030). For both modelling periods, a total of 1872 model runs each were calculated: 3 hydrological variables x 12 months x 2 climate change scenarios (baseline 0K and climate change 3K) x 26 fish species/lifestages (including 14 adult fish species).

The modelled habitat suitability, expressed as WUA (weighted usable area, see section 2.1), reflected the hydraulic changes predicted by the 2D hydrodynamic model, showing the same seasonal pattern for all three hydrological variables Q25, Q50, and Q75 (Fig. 22). Habitat suitability showed negligible differences between the baseline and climate change scenario in winter, spring, and early summer (December to June), with a mean difference for all modelled species and hydrological variables of -0.5% (2021-2030) and -0.7% (2021-2060) and largest differences of -13.1% in late summer and autumn (July to November) in the last 10 years modelling period (2051-2060).

The seasonal pattern differed between two type or groups of fish:

Type 1 potamal often large bodied fish: This type comprises larger bodied species (especially cyprinids, e.g. Silver bream *Blicca bjoerkna*, Common bream *Abramis brama*, Roach, *Rutilus rutilus*) that commonly prefer deeper habitats. The WUA for this group decreases continuously with decreasing water depths in the summer months until a minimum WUA is reached in September. Thereafter (from September until December) the suitability of the study reach increases again continuously for this group of species (Fig. 22).

Type 2 littoral mostly small bodied fish: This group describes the patterns for three smaller bodied fish species (European Minnow *Phoxinus phoxinus*, Threespined Stickleback *Gasterosteus aculeatus*, Tenspined Stickleback *Pungitius pungitius*) that prefer lower water depths and flow velocities. For these three species the WUA increases with decreasing discharge until a local maximum is reached in July. In July a threshold value of the hydraulic habitat conditions with very low discharge and water depths is exceeded and thus, the study reach becomes less suitable. Moreover, otherwise shallow areas close to the banks fall completely dry and thus reduce the available suitable habitat area (expressed as WUA). This pattern is visible in as a local depression of the suitability curve in the months July-October (Fig. 22).
Fig. 22: Habitat suitability (WUA) of the modelled fish species for the three hydrological variables in the Treene study reach.
As the seasonal and species-specific pattern for all three hydrological variables was very similar, only results for the commonly used mean discharge (Q50) will be discussed in more detail in the following.

Species-specific differences were largest for some of the potamal fish species of type 1, with a predicted decrease of the WUA in July to November of up to -78% (Bleak, *Alburnus alburnus*) since WUA was already low in the baseline scenario, and hence, similar decreases in absolute values resulting in much larger relative decreases (percentage values). The minimum WUA, which might act as a bottleneck, already occurred in the baseline scenario for some fish species, and hence climate change possibly will not aggravate the bottleneck (Q50, August-September, common bream, bleak, asp *Aspius aspius*, silver bream). In contrast, for other species of type 1 like pike (*Esox lucius*), roach and perch (*Perca fluviatilis*), minimum values were lower for the climate scenario and potentially act as a new bottleneck.

For the littoral fish species of type 2, the effects of the critical threshold of the hydraulic conditions and consequently the reduced suitability became even more prominent in the climate scenario. Indeed, the habitat suitability was predicted to decrease especially in July to October to lower levels in the climate scenario (e.g.-20 % reduced WUA for European minnow in October, Fig. 22). The largest differences between scenarios for type 2 fish species were predicted in November, when discharge and water depth were higher in the baseline scenario, resulting in a relatively low WUA for the small bodies fish, while the lower discharges predicted for the climate change scenario resulted in more suitable habitat conditions.

In general, the seasonal pattern of habitat suitability for the high (Q25) and low (Q75) conditions was similar to the mean discharge conditions (Q50) described above. For type 1 fish species, the lower and higher discharges in the Q75 and Q25 model, generally translated into lower WUA for the low-water conditions (Q75) and higher WUA for the high-water conditions (Q25), respectively. Furthermore, the distinct local depression in the habitat suitability in summer for the European minnow, threespined stickleback and tenspined stickleback (Type 2) was predicted being stronger under low-flow conditions (Q75) in comparison with mean-flow conditions (Q50). In contrast, the increasing habitat suitability from June until September was higher with higher discharges (Q25) compared to the mean flow conditions (Q50).

For the **land use scenarios**, a total of 7488 model runs each were calculated: 3 hydrological variables x 12 months x 2 climate change scenarios (baseline 0K and climate change 3K) x 4 land use scenarios (baseline, food, energy crops, best practice) x 26 fish species/lifestages (including 14 adult fish species). The following results on the effects of the four land use scenarios are presented exemplarily for four representative fish species (silver bream, Spined loach *Cobitis taenia*, European minnow, roach).

The single effects of different land use scenarios (without the interaction with climate scenarios) show the largest differences for the energy land use scenario (analogous to the predicted discharge changes). In general, the expected effects of the land use scenarios were small with -0.4% for the energy scenario, -0.1% for the Best Practice scenario, and -0.04% for the food land use scenario (mean differences for all modelled species compared to the baseline scenario). As already predicted for the changes in discharge, also the changes in the habitat suitability were negligible in the alternative energy land use scenario (Fig. 23): From December to June, the mean relative differences of the WUA (across all modelled species and hydrological variables) was only -0.2%. In summer and autumn (July to November) the expected differences for energy land use scenario were predicted being larger and showing a reduced suitability of -0.8% (compared to the
baseline) which is even less than the predicted differences in the mean WUA (mean relative differences for 12 months, all modelled species and all hydrological variables) considering the climate change scenarios solely for the periods 2021-2030 (-2.4%) and 2051-2060 (-5.8%).
In conclusion, for the Treene study reach, the changes in the habitat suitability caused by future land use changes will be negligible. In contrast, the effects of reduced discharges due to climate change will generally also be reflected in reduced habitat suitability for all modelled fish species. These negative effects could be detected for species that generally show lower habitat suitability with lower discharges but also for species that usually benefit from lower discharges. For the latter, a critical threshold value of too low discharges was predicted being exceeded during summer, which already caused a lower habitat suitability in these months, which will be even more pronounced under climate change conditions.

Regarding the short-term effects (2021-2030), the changes in the habitat suitability caused by land use change was also predicted being negligible and the changes caused by climate change can be considered small to medium especially during summer and autumn. For the intermediate term (2051-2060), a pronounced species-specific reduction of the habitat suitability caused by similarly marked changes in flow velocity, water depth and available habitat area under climate change conditions can be expected especially during summer and autumn.

However, the analysis also showed that it is difficult to draw general conclusions about the habitat suitability based on hydraulic habitat conditions for the biotic group of fish as a whole since species-specific differences were large. This is especially challenging because (i) fish typically show complex habitat-occurrence relationships (ontogenetic and seasonal habitat shifts, non-continuous and multivariate habitat preferences, critical threshold values) and because (ii) flow velocity and water depth do not change in a similar pattern compared to changes in discharge as a consequence of the natural and asymmetric cross profile of the study reach.

### 3.4.2 Célé study reach

For the Célé 2088 fish habitat suitability models were calculated: 3 hydrological variables x 12 months x 2 climate change scenarios (baseline 0K and climate change 3K) x 29 fish species/life stages (including 16 adult fish species).

The hydraulic changes and seasonal patterns development predicted by the 2D hydrodynamic model were also reflected by the modelled habitat suitability (WUA, Fig. 24).

In winter (December to February/March), the predicted decrease in discharge due to climate change (A2 scenario) caused a clear decline in habitat suitability for 10 out of the 16 modelled adult fish species (e.g. Q50, dace *Leuciscus leuciscus*, gudgeon *Gobio gobio*, pike, spined loach, Fig. 24). In contrast, habitat suitability was predicted to increase for another group of fish (e.g. European minnow, stone loach *Barbatula barbatula*, pumpkinseed *Lepomis gibbosus*, Fig. 24). For a third group, habitat suitability will not change in winter: perch, common carp *Cyprinus carpio* and brown trout *Salmo trutta*. While habitat suitability was predicted to decrease for larger-bodied adult fish during winter (-13.5%), suitability increased for small-bodied and juvenile fish (+24.2%). Overall, the discharge changes in winter resulted in an increase of habitat suitability for all species and life stages of +5.6.
Fig. 24: Habitat suitability (WUA) of the modelled fish species for the three hydrological variables in the Célé study reach.
During the rest of the year (April to November) no such species-specific differences could be detected and habitat suitability was -3.7% lower on average for the climate change scenario. In total, over all modelled fish species, 12 months and three hydrological variables, the habitat suitability (WUA) was predicted being similar between the baseline and the climate scenario (0.01% difference).

In contrast to the Treene River, the climate scenario for the Célé shows the largest differences during winter. Furthermore, results for the Célé differed from the Treene since habitat suitability did not necessarily decline with predicted discharge changes. Instead, especially smaller-bodied species and juvenile life stages did benefit from the predicted lower discharges in winter (December to March, e.g. stone loach, European minnow).

All three hydrological variables (Q25, Q50 und Q75) showed similar species-specific and seasonal patterns with generally the lowest WUA values for the low flow conditions (Q75) and the highest for the high flow conditions (Q25). However, in contrast to the hydraulic input variables (flow velocity and shear stress), these differences between the hydrological variables were not significantly different ($F_{2/1041} = 2.01, p = 0.135$).

In conclusion, in the Célé River the predicted reduced discharge during winter will result in clearly lower habitat suitability for larger-bodied fish species, while smaller-bodied species will benefit from such lower flow conditions. In contrast to the habitat models at the Treene, no threshold limit of too low flow conditions for the small-bodied species is exceeded. The opposed development of habitat suitability for large- and small-bodied species clearly shows again, that it is very difficult to draw general conclusions about the habitat suitability based hydraulic habitat conditions for the biotic group of fish as a whole.
3.5 HABITAT MODEL FOR INVERTEBRATES

(UGE)

3.5.1 HABITAT MODELLING IN THE TREENE AND CÉLÉ STUDY REACH

In the Treene and Célé study reach, the Habitat Evaluation Tool (HET) was applied, which was developed in the IMPACT project (section 2.3.2). It is a univariate, statistical-empirical habitat model that predicts the presence and abundance of invertebrate species within a certain river reach based on empirically derived relationships between habitats (called Habitat Sensitivity Classes) and species presence and abundance (Kiesel et al. 2014). As for fish, in principle, the hydraulic habitat conditions could be used as Habitat Sensitivity Classes but (hydraulic-) habitat specific samples were missing. However, a large number of habitat-specific samples were available for substrates as Habitat Sensitivity Classes since substrate-specific sampling has been conducted in several research projects to develop a standardized Multi-Habitat-Sampling method for the European Water Framework Directive (Hering et al. 2003). Moreover, bottom substratum composition has been widely identified as one of the most significant variables for explaining spatial distribution patterns of benthic invertebrates (Beisel et al. 1998) on a micro scale. Therefore, the HET was applied in the IMPACT project using substrates as Habitat Sensitivity Classes (HSCs).

In the Treene study reach, the effect of discharge changes in the climate and land use scenarios on sediment transport, sorting, and substrate composition was not modelled since bed-substrate mainly consisted of pure sand and no gravel were present which might lead to any sediment sorting that is of relevance for macroinvertebrates. Alternatively, the effect of changes in substrate composition on macroinvertebrates was investigated to assess the sensitivity of the HET modelling results on substrate changes and to assess if different substrate compositions in the range that have to be expected due to discharge changes might significantly affect macroinvertebrates. Only the invertebrate species which already occur in the study reach were considered as model species to assess if the macroinvertebrate assemblage potentially is more strongly affected by substrate changes or if the ecological status can only be significantly improved by the (re-)colonization of existing or new habitats by additional species.

To model the effect of different substrate distributions, all substrates considered in the analysis (Treene n = 9, Célé n = 10) were classified into 4 categories (low, moderate, high, absent) using their present proportion mapped in the study reaches as a baseline (Tab. 1, Tab. 2). Class boundaries were based on expert opinion and considering natural stream-type specific ranges. All possible substrate combinations yielding 100% coverage were modelled, resulting in the same number of composite taxalists which can be considered virtual samples mimicking real-world multi-habitat samples taken in river reaches with different substrate compositions (Treene n = 3561, Célé n = 8247). For each composite taxalist the ecological quality class and a selection of assessment metrics were calculated using the WFD compliant assessment software ASTERICS (Version 4.0.3). The selected assessment metrics were pooled in five groups: (i) general assessment metrics indicating the ecological status (EQR), (ii) streamtype-specific assessment metrics (Core-metrics), (iii) diversity metrics, (iv) feeding types, and (v) taxonomical groups (see Tab. 3, Tab. 4).
Tab. 1: Considered substrates and class boundaries for the Treene study reach.

<table>
<thead>
<tr>
<th>%cover</th>
<th>Gravel</th>
<th>Silt/Loam</th>
<th>Organic matter</th>
<th>Sand/Mud</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>akal</td>
<td>argylal</td>
<td>cpom</td>
<td>xylal</td>
</tr>
<tr>
<td>Low</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Moderate</td>
<td>20</td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>High</td>
<td>40</td>
<td>20</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>Absent</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Tab. 2: Considered substrates and class boundaries for the Treene study reach.

<table>
<thead>
<tr>
<th>%cover</th>
<th>Sand</th>
<th>Organic matter</th>
<th>Rip. vegetation</th>
<th>Dead wood</th>
<th>Large stones</th>
<th>Small stones</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>psam</td>
<td>cpom</td>
<td>fpom</td>
<td>pelal</td>
<td>lptp</td>
<td>xylal</td>
</tr>
<tr>
<td>Low</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Moderate</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>High</td>
<td>20</td>
<td>20</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>15</td>
</tr>
<tr>
<td>Absent</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
The ecological status resulting from the substrate combinations was either good or moderate in the Treene study reach and either high or good in the Célé study reach (Fig. 25). The substrate combinations resulting in a good ecological status in the Treene study reach had a higher percentage coverage of gravel and a lower coverage of organic matter compared to the substrate combinations only resulting in a moderate ecological status. These results indicated that there would be a higher probability to reach good ecological status in the Treene study reach if gravel substrates were present and the coverage of organic matter reduced. In the Célé study reach, a high ecological status resulted from an intermediate amount of organic matter, a higher amount of deadwood, and an intermediate amount of large lithal fractions. A good ecological status was related to an increased amount of silt and organic matter, and a smaller amount of deadwood and large stones. Overall, the effect of the different substrate clusters on the ecological quality was modest. Changes in the ecological status only resulted from drastic changes in substrate compositions or by the complete omission of certain substrate components. These results indicated that changes of the ecological status will probably not occur assuming that discharge changes will not result in substrate compositions which are that different from the present conditions.

![Figure 25](image-url)

Fig. 25: Percentage coverage of the substrates in substrate combinations resulting in good and moderate (A = Treene) and high and good (B = Célé) ecological status.
The relative importance / influence of the different substrates for the different biological metrics was quantified using Boosted Regression Trees (BRT). Regression trees split the dataset in sub-datasets using one single predictor variable (here substrate) at each split and trying to maximise the difference between the sub-datasets in respect to the response variable (here biological metric), i.e. to maximize the between-groups sum-of-squares. A boosted regression tree model consists of a sequence of single regression trees, where each successive tree after the first one is built using the residuals of the preceding tree. The final BRT model is a linear combination of many trees that can be thought of as a regression model to predict the response variable (here biological metric) where each term is a tree. The relative importance of the predictor variables is calculated based on the number of times a variable is selected for splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all trees. The relative influence (or contribution) of each variable is scaled so that the sum adds to 100, with higher numbers indicating stronger influence on the response (negative, positive or both). The general direction of the relationship (negative or positive) was derived from a simple correlation matrix.

Tab. 3 : Relative Importance (Boosted Regression Trees) of substrates for different metrics in the Treene study reach. For metric explanation see ASTERICS Software Handbook (Version 4, 2013).

<table>
<thead>
<tr>
<th>General metrics</th>
<th>Gravel</th>
<th>Silt/Loam</th>
<th>Organic matter</th>
<th>Sand/Mud</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ecological quality class</td>
<td>38.6 (-)</td>
<td>2.3 (+)</td>
<td>37.6 (+)</td>
<td>21.5 (-)</td>
</tr>
<tr>
<td>Score general degradation</td>
<td>91.1 (+)</td>
<td>0.8 (-)</td>
<td>4.5 (-)</td>
<td>3.6 (-)</td>
</tr>
<tr>
<td>ASPT</td>
<td>96.4 (+)</td>
<td>0.3 (-)</td>
<td>2.2 (-)</td>
<td>1.1 (-)</td>
</tr>
<tr>
<td>Core metrics</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fauna Index</td>
<td>82.1 (+)</td>
<td>2.2 (-)</td>
<td>9.4 (-)</td>
<td>6.4 (-)</td>
</tr>
<tr>
<td>% Litoral taxa</td>
<td>28.1 (-)</td>
<td>5.1 (+)</td>
<td>7.1 (-)</td>
<td>59.7 (+)</td>
</tr>
<tr>
<td>% EPT</td>
<td>14.3 (+)</td>
<td>43.2 (-)</td>
<td>28.9 (-)</td>
<td>13.6 (+)</td>
</tr>
<tr>
<td>Number of Trichoptera</td>
<td>99.0 (+)</td>
<td>0.0 (-)</td>
<td>1.0 (-)</td>
<td>0.0 (-)</td>
</tr>
<tr>
<td>Diversity metrics</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Evenness</td>
<td>65.6 (-)</td>
<td>2.2 (+)</td>
<td>12.4 (+)</td>
<td>19.9 (-)</td>
</tr>
<tr>
<td>Margalef Index</td>
<td>95.6 (+)</td>
<td>0.2 (-)</td>
<td>4.1 (-)</td>
<td>0.1 (-)</td>
</tr>
<tr>
<td>Shannon Index</td>
<td>19.3 (+)</td>
<td>1.8 (+)</td>
<td>11.1 (+)</td>
<td>67.9 (-)</td>
</tr>
<tr>
<td>Simpson Index</td>
<td>6.6 (-)</td>
<td>52.7 (+)</td>
<td>17.6 (-)</td>
<td>23.1 (+)</td>
</tr>
<tr>
<td>Feeding types</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Active filterers</td>
<td>3.7 (+)</td>
<td>0.9 (+)</td>
<td>88.9 (-)</td>
<td>6.4 (+)</td>
</tr>
<tr>
<td>% Gatherers/Collectors</td>
<td>14.9 (-)</td>
<td>1.2 (+)</td>
<td>76.2 (+)</td>
<td>7.7 (-)</td>
</tr>
<tr>
<td>% Grazer/Scraper</td>
<td>89.8 (+)</td>
<td>0.1 (-)</td>
<td>2.0 (-)</td>
<td>8.1 (-)</td>
</tr>
<tr>
<td>% Passive Filterers</td>
<td>2.0 (-)</td>
<td>0.6 (-)</td>
<td>84.4 (+)</td>
<td>12.9 (-)</td>
</tr>
<tr>
<td>% Predators</td>
<td>4.2 (-)</td>
<td>1.2 (+)</td>
<td>72.7 (+)</td>
<td>21.9 (-)</td>
</tr>
<tr>
<td>% Shredders</td>
<td>0.7 (-)</td>
<td>35.0 (-)</td>
<td>60.2 (+)</td>
<td>4.0 (-)</td>
</tr>
<tr>
<td>Taxonomic groups</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Bivalvia</td>
<td>6.9 (+)</td>
<td>0.5 (+)</td>
<td>90.6 (-)</td>
<td>2.0 (+)</td>
</tr>
<tr>
<td>% Coleoptera</td>
<td>6.5 (+)</td>
<td>76.4 (-)</td>
<td>1.8 (+)</td>
<td>15.3 (-)</td>
</tr>
<tr>
<td>% Crustacea</td>
<td>5.7 (+)</td>
<td>23.7 (-)</td>
<td>10.3 (+)</td>
<td>60.3 (-)</td>
</tr>
<tr>
<td>% Diptera</td>
<td>44.4 (-)</td>
<td>6.4 (+)</td>
<td>16.6 (-)</td>
<td>32.6 (+)</td>
</tr>
<tr>
<td>% Gastropoda</td>
<td>81.6 (+)</td>
<td>5.7 (+)</td>
<td>2.1 (-)</td>
<td>10.5 (-)</td>
</tr>
</tbody>
</table>
In this study, the relative importance is a measure to describe the sensitivity of a biological metric towards changes of a specific substrate component, considering both, a positive and negative effect. The higher the relative importance, the more sensitive the metric responds to changes in the respective substrate cluster. In the Treene study reach, most biological metrics were most strongly affected by changes in the coverage of gravelly substrates, especially the general, final assessment scores, and organic matter was an important predictor for the feeding types (i.e. have the highest values in the respective rows in Tab. 3). In contrast, riparian vegetation was the most important predictor for the general, final and other assessment scores, and organic matter affected many diversity metrics and feeding types (i.e. have the highest values in the respective rows in Tab. 4).

Tab. 4: Relative Importance (Boosted Regression Trees) of substrates for different metrics in the Célé study reach. For metric explanation see ASTERICS Software Handbook (Version 4, 2013).

<table>
<thead>
<tr>
<th>General</th>
<th>Sand</th>
<th>Organic matter</th>
<th>Riparian vegetation</th>
<th>Deadwood</th>
<th>Large stones</th>
<th>Small stones</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ecological quality class</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>na</td>
</tr>
<tr>
<td>Score general degradation</td>
<td>1.7</td>
<td>28.3</td>
<td>57.2</td>
<td>8.5</td>
<td>4.0</td>
<td>0.2</td>
</tr>
<tr>
<td>ASPT</td>
<td>0.5</td>
<td>21.2</td>
<td>77.6</td>
<td>0.6</td>
<td>0.1</td>
<td>0.0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Assessment metrics</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>% Metarthiral taxa</td>
<td>0.7</td>
<td>42.6</td>
<td>9.3</td>
<td>6.6</td>
<td>40.1</td>
<td>0.6</td>
</tr>
<tr>
<td>Rheoindex</td>
<td>0.2</td>
<td>4.6</td>
<td>93.4</td>
<td>0.7</td>
<td>0.7</td>
<td>0.3</td>
</tr>
<tr>
<td>% EPT</td>
<td>2.0</td>
<td>87.0</td>
<td>2.7</td>
<td>0.9</td>
<td>6.7</td>
<td>0.6</td>
</tr>
<tr>
<td>Number of EPTCBO</td>
<td>0.1</td>
<td>6.6</td>
<td>74.8</td>
<td>18.5</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Fauna Index</td>
<td>0.4</td>
<td>5.7</td>
<td>82.8</td>
<td>10.2</td>
<td>0.5</td>
<td>0.4</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Diversity metrics</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Eveness</td>
<td>2.9</td>
<td>63.8</td>
<td>23.3</td>
<td>4.8</td>
<td>3.0</td>
<td>2.1</td>
</tr>
<tr>
<td>Margalef Index</td>
<td>0.8</td>
<td>13.5</td>
<td>73.5</td>
<td>10.5</td>
<td>1.5</td>
<td>0.2</td>
</tr>
<tr>
<td>Shannon Index</td>
<td>0.0</td>
<td>48.3</td>
<td>33.0</td>
<td>0.5</td>
<td>11.1</td>
<td>7.0</td>
</tr>
<tr>
<td>Simpson Index</td>
<td>0.4</td>
<td>42.3</td>
<td>26.6</td>
<td>0.2</td>
<td>22.0</td>
<td>8.5</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Feeding types</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>% Active filters</td>
<td>16.1</td>
<td>11.1</td>
<td>2.0</td>
<td>0.7</td>
<td>69.9</td>
<td>0.2</td>
</tr>
<tr>
<td>% Gatherers/Collectors</td>
<td>24.5</td>
<td>4.1</td>
<td>1.2</td>
<td>7.1</td>
<td>14.3</td>
<td>48.8</td>
</tr>
<tr>
<td>% Grazers/Scrapers</td>
<td>0.1</td>
<td>57.3</td>
<td>10.4</td>
<td>0.1</td>
<td>20.1</td>
<td>12.0</td>
</tr>
<tr>
<td>% Passive Filters</td>
<td>0.9</td>
<td>60.0</td>
<td>11.9</td>
<td>1.0</td>
<td>23.4</td>
<td>2.7</td>
</tr>
<tr>
<td>% Predators</td>
<td>9.0</td>
<td>7.4</td>
<td>27.4</td>
<td>1.5</td>
<td>37.1</td>
<td>17.5</td>
</tr>
<tr>
<td>% Shredders</td>
<td>1.9</td>
<td>26.8</td>
<td>7.6</td>
<td>1.2</td>
<td>57.8</td>
<td>4.7</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Taxonomic groups</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>% Bivalvia</td>
<td>45.2</td>
<td>0.1</td>
<td>0.0</td>
<td>0.0</td>
<td>51.9</td>
<td>2.7</td>
</tr>
<tr>
<td>% Coleoptera</td>
<td>0.2</td>
<td>79.2</td>
<td>12.2</td>
<td>2.5</td>
<td>1.2</td>
<td>4.7</td>
</tr>
<tr>
<td>% Crustacea</td>
<td>0.2</td>
<td>86.8</td>
<td>8.5</td>
<td>0.2</td>
<td>3.5</td>
<td>0.8</td>
</tr>
<tr>
<td>% Diptera</td>
<td>3.4</td>
<td>48.9</td>
<td>7.5</td>
<td>0.5</td>
<td>33.9</td>
<td>5.7</td>
</tr>
<tr>
<td>% Gastropoda</td>
<td>0.1</td>
<td>14.2</td>
<td>9.5</td>
<td>0.3</td>
<td>72.9</td>
<td>2.8</td>
</tr>
</tbody>
</table>
3.5.2 COMBINING INFORMATION OF THE HABITAT MODEL AND ON NUTRIENT LOADS

For macroinvertebrates, the results of the habitat (3.5.1) and water quality (3.1) modelling were quantitatively linked to assess species presence and abundance in the Treene study reach (water quality was not modelled for the Célé catchment). First, the presence and abundance of macroinvertebrate species was modelled using the HET based on the habitat (substrate) composition. Second, species abundance values predicted by the HET were multiplied by a factor which was derived from dose-response relationships between macroinvertebrate abundance and nutrient concentrations to correct species abundance for the nutrient effect (see paragraph on final assessment in section 2.1). This either leads to an increase (factor > 1), decrease (factor < 1) or to unchanged abundance values (factor = 1).

The derivation of the empirical relationship between the abundance of individual species and the nitrate concentration (dose-response relationships) was based on data taken from the German Federal Environment Agency (UBA) database (Dahm et al. 2014). Eight out of the species occurring in the study reach were present in at least 30 samples in the database, which was the minimum number to derive statistically robust dose-response relationships. Unfortunately, these 8 species did not overlap with the 10 species for which dispersal models could be developed (section 3.7). For the 8 model species, abundance and nutrient (NO$_3$) values of all samples taken in the respective stream type of the Treene river (German stream type 15, sand-dominated lowland rivers) were extracted from the database and separate sub-datasets for each species were created. Based on these data, dose-response-curves were derived that describe how the abundance of a species changes with increasing nutrient concentrations in comparison with the present-state concentration in 2011. Based on the dose-response-curves, factors were derived to correct the modelled abundances with regard to the modelled nitrate concentrations (for more details see Guse et al. in prep.).

Based on the results of the HET, the dose-response curves and resulting correction factors, as well as the modelled nitrate concentrations for the different climate change and land use scenarios, the presence and abundance of macroinvertebrates was assessed. For the HET, the substrate conditions mapped in the study reach were used (10% Silt/Loam, 20% organic matter, 70% sand) since no substrate changes have to be expected since bed-substrate mainly consisted of pure sand and no gravel were present which might lead to any sediment sorting relevant for macroinvertebrates. The nitrate concentrations were calculated based on the modelled daily values of the four land use scenarios (Base, Food, Energy, Best) and two climate scenarios (0K, 3K) for the modelling period 2021-2030. Mean nitrate concentrations were calculated for the period from March 1st to March 7th (Tab. 5) since this did correspond to the time the macroinvertebrate samples had been taken.

For each species and scenario, the mean relative difference over the whole modelling period (2021-2030) were calculated, i.e. the mean relative difference between the abundance predicted by the HET model (i.e. based on the mapped substrate conditions, and nutrient concentrations of the baseline scenarios), and the abundance corrected by the respective factor (i.e. assuming constant substrate conditions and nutrient concentrations of the different scenarios) (since substrate conditions have been assumed constant, the mean relative difference corresponds to the mean of the correction factors over all ten years of the modelling period).

In all three land use and the 3K climate change scenario, the abundance of virtually all species was predicted to change only slightly (Fig. 26), except for Tanypodinae Gen. sp. The abundance of
all other species was predicted to change by less than 15.9% in all scenarios. Predicted changes were especially low in the food scenario, where relative differences of the abundance values of the seven species (i.e. excluding *Tanypodinae* Gen. sp) ranged from -2.5% to +2.9% compared to higher ranges in the Energy (-7.8% to 3.5%), Best Practice (-12.9 to 6.7), and 3K scenario (-15.9 to -2.3%).

The largest species-specific changes were predicted for *Tanypodinae* Gen. sp, in the Best Practice scenario with a mean increase of the abundance over the ten years modelling period by +30.7%. For two species (*Calopteryx splendens*, *Sialis lutaria*), the largest changes were predicted in the 3K climate change scenario with a decrease by -12.5% and -15.9%, respectively, while the largest decrease in abundance of *Gammarus pulex* (-12.9%) was predicted for the Best Practice scenario. The other four species (*Chironomini Gen. sp.*, *Erpobdella octoculata*, *Pisidum sp.*, *Prodiamesa olivaeca*) showed no distinct differences between scenarios and only slight changes (< 7.8%).

In summary, it can be concluded that the effect of nitrate was predicted to considerably differ between species and that there was no general pattern or trend. While some species will probably benefit from higher nutrient levels, the abundances of other species were predicted to decrease. With that being said, it is important to consider the "importance" of each species for a certain river type. In this context, a negative impact on reference species should be prevented in the first place. For this study, the effects of increasing nitrate concentrations could not be assessed for reference species, as none of them was included in the analysis due to the lack of species data and nutrient measurements.

### Tab. 5: Mean nitrate concentrations for different land use and climate scenarios

<table>
<thead>
<tr>
<th>Year</th>
<th>Date</th>
<th>NO3 (mg/l)</th>
<th>NO3 (mg/l)</th>
<th>NO3 (mg/l)</th>
<th>NO3 (mg/l)</th>
<th>NO3 (mg/l)</th>
<th>NO3 (mg/l)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2021</td>
<td>1-7.03.</td>
<td>6.60</td>
<td>6.74</td>
<td>5.75</td>
<td>5.27</td>
<td>6.68</td>
<td>5.24</td>
</tr>
<tr>
<td>2022</td>
<td>1-7.03.</td>
<td>4.90</td>
<td>4.95</td>
<td>4.39</td>
<td>3.97</td>
<td>4.95</td>
<td>4.83</td>
</tr>
<tr>
<td>2023</td>
<td>1-7.03.</td>
<td>4.65</td>
<td>4.81</td>
<td>3.94</td>
<td>3.65</td>
<td>4.67</td>
<td>4.38</td>
</tr>
<tr>
<td>2024</td>
<td>1-7.03.</td>
<td>5.01</td>
<td>5.15</td>
<td>4.20</td>
<td>3.86</td>
<td>5.08</td>
<td>4.77</td>
</tr>
<tr>
<td>2025</td>
<td>1-7.03.</td>
<td>2.52</td>
<td>2.60</td>
<td>2.21</td>
<td>2.18</td>
<td>2.55</td>
<td>4.26</td>
</tr>
<tr>
<td>2026</td>
<td>1-7.03.</td>
<td>4.92</td>
<td>5.02</td>
<td>4.41</td>
<td>4.01</td>
<td>5.00</td>
<td>4.46</td>
</tr>
<tr>
<td>2027</td>
<td>1-7.03.</td>
<td>5.24</td>
<td>5.34</td>
<td>4.40</td>
<td>3.90</td>
<td>5.30</td>
<td>5.85</td>
</tr>
<tr>
<td>2028</td>
<td>1-7.03.</td>
<td>5.00</td>
<td>5.26</td>
<td>3.87</td>
<td>3.56</td>
<td>5.05</td>
<td>6.20</td>
</tr>
<tr>
<td>2029</td>
<td>1-7.03.</td>
<td>7.73</td>
<td>8.12</td>
<td>6.52</td>
<td>5.97</td>
<td>7.85</td>
<td>5.59</td>
</tr>
<tr>
<td>2030</td>
<td>1-7.03.</td>
<td>7.98</td>
<td>8.20</td>
<td>6.46</td>
<td>5.50</td>
<td>8.13</td>
<td>5.82</td>
</tr>
</tbody>
</table>
Fig. 26: Relative differences of the abundances of the eight model species in the three land use and the climate change scenario compared to the respective baseline scenario (Guse et al. in prep.).
3.6 DISPERALAL MODEL FOR FISH

3.6.1 TREENE RIVER NETWORK – GIS DISPERSAL MODELLING (IGB)

As discussed in section 2.3.2, the number of source populations is potentially underestimated when using field sampling data while it is overestimated using SDMs. Consequently, for the fish dispersal modelling at the Treene and Célè, both methods to identify source populations were used in separate model runs. This allowed to account for the methodological uncertainty caused by the approach to identify source populations.

Identification of source populations

Species Distribution Models (SDM) were used in the Treene catchment to determine potential source populations. The SDMs generally performed well with good to moderate cross-validated model results (AUC, area under receiver-operator curve). The presence/absence of 13 species was modelled based on hydromorphological data and river network characteristics using the statistical modelling algorithm Boosted Regression Trees. The State Agency for Agriculture, Environment and Rural Areas (LLUR), Schleswig Holstein, kindly provided data on fish sampled at 81 sites between 2004 and 2011, GIS data of the river network, and hydromorphological data to described the habitat characteristics (data of a hydromorphological survey covering the whole river network which is similar to the on-site survey of the Länderarbeitsgemeinschaft Wasser (LAWA) described in Gellert et al. (2014) and includes information on migration barriers.

The environmental predictor dataset can be divided into: (i) measured variables that quantitatively describe channel features and characteristics (e.g. flow velocity, depth and width, substrates, number of riffles and pools, sinuosity) and (ii) assessment variables that describe specific aspects of the channel in relation to stream-type specific natural reference conditions (functional units). In addition, three stream topological variables were included in the SDMs: the Strahler stream order, Shreve stream order and the distance from the mouth.

The hydromorphological state was not only described for the fish sampling site but also for the up- and downstream river network in four predefined distance classes (using a GIS neighbourhood filter tool GRASS GIS, r.rdfilter) to account for the mobility of fish and the use of habitats within their home range by calculating average values at four predefined distances. This so-called focal filter works like a low pass filter where parameter values of adjacent cells in a given distance are averaged and the mean or median value of this new focal predictor is assigned to the focal centre cell. For this analysis, all model grid cells in the predefined distance (0.2, 1.0, 2.5, 4.0 km) up- as well as downstream of the fish sampling sites were used to calculate mean and median focal predictors for continuous and categorical variables respectively.

In total, 260 SDMs were calculated: 2 groups of environmental data (measured vs. assessment) x 2 (with/without) topological variables x 5 focal distance classes x 13 fish species.

The model quality was not significantly related to the group of environmental data (measured vs. assessment). In contrast, including topological variables (stream order) generally improved the model quality, independent from the environmental dataset and the focal distance. Furthermore, model quality was greatly improved by including additional information on the habitat...
characteristics up- and downstream of the sampled site (focal predictors). The highest AUC values and thus the best statistical relationship between the occurrence of a species and the habitat was achieved by including information at a distance of 2.5 km up- and downstream (total length 5.0 km, Fig. 27).

For all 260 SDMs, maps indicating the logistic probability of occurrence of the 13 single species in the grid cells of the river network were calculated. Subsequently, 20 probability maps for each of the 13 modelled species were AUC-weighted averaged. The so created 13 species-specific probability maps were transformed into a binary (presence/absence) map using a commonly used objective threshold that maximizes the sum of sensitivity (true positive rate) and specificity (true negative rate). This threshold achieves the maximum correctly predicted presences and absences in the final binary output map. The final predicted presence maps were subsequently used as species-specific source populations for the species dispersal model FIDIMO.

**Results FIDIMO**

In total, 280 fish dispersal models were calculated for the Treene catchment: 13 fish species based on SDM / 15 fish species based on field sampling data x 3 consecutive modelled yearly time steps x 3 statistical confidence intervals (FIDIMO output, 95%) for the last modelled time step x each model with and without migration barriers.

The model results, expressed as the share of the river network which is reachable in the modelling time-period and referred to as re-colonization potential in the following, did more strongly depend on the method used to identify the source populations (sampling data vs. SDM) than on the migration barriers. The re-colonization potential was 18.4% higher using SDMs as source populations (68.0% excl. barriers) compared to models using sampling points (49.6% excl. barriers). Thus, the re-colonization potential was generally lower when sampling data were used compared to SDM (as hypothesized in section 2.3.2) but both methods provided results in the same order of magnitude. In contrast to the relatively large effect of source populations, the re-colonization potential only dropped by -3.6 and -3.5 percentage points if barriers were included in the SDM models (64.4% incl. barriers) and for models based on field sampling data (46.1% incl. barriers).
The differences between the two methods to identify source populations were species-specific. The largest differences were detected for ten-spined stickleback (+63% for SDM) and roach (-23% for SDM), while ruffe (Gymnocephalus cernuus, +0.8%), perch (+1.6%) and European eel (Anguilla anguilla, -2.0%) showed the smallest differences between SDM and sampling data as input source populations.

Similarly, the effect of barriers also was species-specific. Including barriers reduced the re-colonization potential on average by only -3.6% (for SDMs) and -3.5% (for sampling data), respectively. Migration barriers had the largest negative effect on larger species with relatively high dispersal abilities (see 2.3.2) like Salmon (Salmo salar, -19%), roach (-7%), perch (-7%) and eel (-6%). For all other species, the effect of barriers on the re-colonization potential was less than -3%.

A species-specific analysis of the FIDIMO results revealed that re-colonization potential in the Treene catchment was largest for eel (100%), brown trout (94%) and salmon (92%) (based on SDM, excl. barriers), probably due to a combination of their high dispersal abilities and the presence of source populations. In addition, some other species also had a high re-colonization potential as a consequence of the large number of source populations (60% presence in the...
catchment) rather than due to their dispersal abilities (gudgeon 77%, three-spined stickleback 67%, ten-spined stickleback 88%). In contrast, small-bodied and rare species had the lowest re-colonization potential like ruffe (18%), spined loach (27%), and minnow (42%, Fig. 28).

### 3.6.2 CÉLÉ RIVER NETWORK – GIS DISPERSAL MODELLING

(IGB)

**Identification of source populations**

SDMs for 14 species in the Célé catchment were calculated based on (bio)climatic variables which were provided by UPS. In addition, fish sampling data were available at 24 sampling sites along the main stem of the Célé river and were used as potential source populations for modelling fish dispersal of four selected species (chub, *Squalius cephalus*; gudgeon, dace, and minnow). Therefore, the number of fish sampling sites was markedly lower in the Célé river network (0.08/km) compared to the Treene river network (0.24/km) and offered the opportunity to investigate the influence of available sampling data on the results of dispersal models.

**Results FIDIMO**

In total, 180 fish dispersal models were calculated for the Célé catchment: 14 fish species based on SDM / 4 fish species based on field sampling data x 3 consecutive modelled yearly time steps x 3 statistical confidence intervals (FIDIMO output, 95%) for the last modelled time step x each model with and without migration barriers.

In comparison with the Treene, the re-colonization potential in the Célé river network depended much more on the method to identify source populations. For four out of the 14 fish species, source populations were identified based on SDMs and sampling data. For these four fish species, the re-colonization potential was 45.0 percentage points higher using SDMs as source populations (64.4% excl. barriers) compared to models using sampling points (19.4% excl. barriers). European minnow (+64% for SDMs) and dace (+19.8% for SDMs) showed the largest and smallest differences, respectively. These results indicated that the sampling point density at the Célé river was too low to be used as source populations in a dispersal model and future applications of FIDIMO using fish samples as source populations should be in the range of the sampling point density used for the Treene to give reliable and similar results to models using SDMs.

Similarly to the Treene river network, the re-colonization potential only dropped by -0.1 and -0.9 percentage points if barriers were included in the SDM models (64.3% incl. barriers) and for models based on field sampling data (18.5% incl. barriers). These results indicated that in both river networks, the number and location of source populations had a much higher influence on the re-colonization potential compared to migration barriers. These results indicated that protecting and establishing source populations probably will have an even greater effect on the biological state and restoration success than restoring river continuity. Therefore, it is recommended that river management should focus on source populations which have not been adequately considered in the past, besides restoring river continuity.

On average over all 14 modelled fish species, 57% of the Célé catchment can potentially be approached using SDMs as source populations and when barriers are excluded from the analysis (Fig. 29). When migration barriers are included in the model, the dispersal potential is reduced by -4.5% comparable to the effect of barriers in the Treene (-3.6%).

60
A species-specific analysis of the FIDIMO results revealed that large species with high dispersal abilities (brown trout 100%; chub 78%; common carp 76%) and small-bodied species with a large number of source populations (e.g. minnow 75%) exhibit the greatest re-colonization potential of all modelled species in the Célé (Fig. 29). In contrast, small-bodied species with fewer source populations show the lowest dispersal potential of all modelled species after three modelled years (bullhead *Cottus gobio*, 18%; pumkinseed 29%).

**Fig. 29**: Species-specific re-colonization potential (share of river network reachable) for dispersal models using sampling points vs. SDMs as source populations and including vs. excluding barriers. In addition the share of the river network already occupied by the source populations predicted by the SDM is given (Célé river network).
3.6.3 **CÉLÉ RIVER NETWORK – GENETIC ANALYSIS**

(UPS)

An important component of the IMPACT project concerns the assessment of movements and dispersal of freshwater organisms (macroinvertebrates and fish). Comparing the molecular-based estimates of dispersal with the data from the literature review and the GIS dispersal modelling approach (2.3.2) provided important fundamental insights about the dispersal of fish species in rivers.

The aims of the following section are threefold: (i) characterizing the **spatial distribution of the genetic diversity** of four freshwater fish species (i.e. the chub *Squalius cephalus*, the Languedoc gudgeon *Gobio occitaniae*, the stone loach *Barbatula barbatula* and the common minnow *Phoxinus phoxinus*) at the whole Garonne river basin level (South-Western France), (ii) approximating **migration rates and dispersal asymmetry rates** at the river basin scale for each species using model-based genetic inference methods, and (iii) determining **dispersal rates** and the **distance travelled by dispersers** for each species at the Célé river scale using genetic assignment methods.

**Description of the spatial distribution and patterns of genetic diversity.**

We first developed a microsatellite genetic database for four freshwater fish species (i.e. *Squalius cephalus*, *Gobio occitaniae*, *Barbatula barbatula* and *Phoxinus phoxinus*) that were sampled during Spring/Summer 2010 and 2011 at 92 sampling sites distributed across the whole Garonne river basin (South-Western France; Fig. 30). Up to 25 individuals per species and per site were sampled. It is noteworthy that not all species were present at all sampling sites (Fig. 30) and some species were at a density that did not allow reaching the objective of 25 individuals. In such cases, we captured as many individuals as possible to allow consistent genetic analyses (Paz-Vinas *et al.* in prep). Data from two supplementary fish species were also gathered during the IMPACT project (i.e. for the threatened fish *Parachondrostoma toxostoma* and for the endemic Cyprinid *Leuciscus burdigalensis*). These two species have not been included in the genetic dispersal approach because of the low number of successfully sampled sites. However, we combined the genetic data obtained for *Parachondrostoma toxostoma* with long-term demographic data from a monitoring survey realized by the French partner ONEMA to improve conservation planning for this species (Paz-Vinas *et al.* 2013a).
We then assessed the spatial distribution of the genetic diversity of *Squalius cephalus*, *Gobio occitaniae*, *Barbatula barbatula* and *Phoxinus phoxinus* at the Garonne river basin level by calculating different descriptive statistics such as the allelic richness (hereafter, AR; Petit *et al.* 1998) or Jost's D (a measure of genetic differentiation, hereafter $D_{EST}$; Jost 2008). We put a particular emphasis on identifying spatial patterns of genetic diversity such as patterns of Isolation by Distance (IBD; Wright 1943) and Increases in Genetic Diversity Downstream (IGDD; Paz-Vinas *et al.* submitted). Indeed, spatial patterns of genetic diversity such as IBD and IGDD are the genetic by-product of one or many interacting processes that shape genetic diversity at the meta-population level (Paz-Vinas *et al.* submitted). For instance, IGDD, which is a general pattern of genetic diversity in rivers that holds true for many taxa (Paz-Vinas *et al.* submitted), can be the produce of (i) an increase in effective population sizes (hereafter, $N_e$) along the upstream-downstream gradient, (ii) upstream-directed colonization processes, or (iii) downstream-biased gene flow. The identification of the process(es) generating empirical IGDD is
mandatory when looking for dispersal parameters inference (Paz-Vinas et al. 2013b). As each process lead specific genetic footprints that are captured by different summary statistics of the genetic diversity (Paz-Vinas et al., submitted), it is thus possible to make use of these differential footprints under specific genetic-based inferential frameworks to disentangle the underlying processes –and associated parameter values– behind observed spatial pattern of genetic diversity.

Our results show that two out of the four species (i.e. *S. cephalus* and *G. occitaniae*) display significant patterns of IGDD, as indicated by the significant and negative Pearson’s correlations between Allelic Richness (*AR*) and topological distance of sampling sites from the Garonne river mouth (*Fig. 31*). These two species also displayed significant negative correlations between *AR* and longitude, and *G. occitaniae* also displayed a significant pattern of increase in *AR* with latitude (*Fig. 31*). It is noteworthy that the four species also exhibited different patterns of genetic diversity for other summary statistics of the genetic diversity such as the $D_{EST}$ (data not shown; Paz-Vinas et al. in prep).

Regarding patterns of Isolation By Distance (IBD), we detected general increases in pairwise genetic differentiation as the topological distance between pairs of sites increases. This is what is expected when dispersal is geographically limited. IBD can be used to determine the geographic distance at which dispersal becomes limited. Limited dispersal is generally indicated (graphically) by (i) a breaking point in the slope of the IBD and/or (ii) a sudden increase in variance (for a given geographic distance) regarding genetic differentiation (which indicates that genetic drift becomes much more important than gene flow for explaining pairwise genetic differentiation). Following these two criteria, a dispersal limitation was detected for two species (e.g. *B. barbatula* and *P. phoxinus*, see *Fig. 31B3-4*) and was around 1-200 km. For *G. occitanae*, there was a relatively clear breaking point (around 2-300 km, *Fig. 31B2*), although the increase in variance was less evident, hence indicating that the dispersal limitation was much more difficult to infer for this species. There was finally no clear pattern of dispersal limitation regarding *S. cephalus*, which may indicate that these species is not limited in its dispersion.

To summarize, these results show that the observed patterns of genetic diversity for these species in the Garonne river basin are different (i) at the inter-specific level for a given metric, (ii) at the intra-specific level, between different metrics, and that (iii) IBD provides information on the overall dispersal capacities displayed by these fish species, although not accurately. In order to provide more accurate parameter estimates regarding the dispersal of these fish species, we then used model-based genetic inference procedures that allow accounting for all the processes that may explain the patterns we observed.
Fig. 31: Maps representing the spatial distribution of interpolated values of AR, (A), and the Isolation By Distance patterns (B) for Squalius cephalus, Gobio occitaniae, Barbatula barbatula, and Phoxinus phoxinus (1, 2, 3, 4 respectively in the figure) in the Garonne river basin. The cursor on the vertical colored scale for (A) indicates the mean value of AR. The correlation values (and their significance) between these statistics and topological distance to the river mouth, latitude and longitude are also reported. Regression models in (B) fit segmented relationships between pairwise genetic differentiation and the topological distance between sites (vertical lines indicate break-point estimates).
Approximating dispersal-related parameters at the Garonne river basin scale.

We implemented model-based genetic inference procedures to approximate, for each species at the Garonne river basin scale, the mean values of upstream- and downstream-directed migration rates, as well as the mean asymmetry dispersal rates (i.e. the ratio between mean downstream-directed and upstream-directed mean migration rates). The aim of this modelling approach is to shed light on the global dispersal regimes and capacities displayed by these four species at a large spatial scale (i.e. the river basin scale).

We specifically applied approximate Bayesian computation procedures (hereafter ABC; Beaumont et al. 2002). Briefly, ABC methods are statistical inferential procedures based on the comparison of many simulated genetic datasets generated under one (or many) complex demographic/evolutionary models with observed empirical data. This comparison is not based on raw genetic data (e.g. individuals’ genotypes), but rather on easy-to-estimate descriptive statistics (e.g. AR, heterozygosities or D<sub>EST</sub>). These methods have been proven powerful to (i) determine which model among a set of likely evolutionary models best explains observed data (“model-choice” procedures), and (ii) infer key demographic and evolutionary parameters for a given model, such as effective population sizes, migration rates or dispersal asymmetry rates (Beaumont et al. 2002; Csilléry et al. 2012).

Here, we applied ABC procedures by considering complex evolutionary models that are spatially structured in a dendritic fashion, as it is the case for river networks (Figure 3). We then simulated microsatellite genetic datasets under different dendritic models that were ruled by one, two or three potentially interacting processes: downstream-biased asymmetric gene flow, differential in N<sub>e</sub> along an upstream-downstream gradient, and upstream-directed colonization (Fig. 32).

A first implementation of ABC model-choice procedures highlighted that the model that better fits with empirical genetic data observed for the four fish species is the one that implements the three processes mentioned above at the same time (i.e. downstream-biased asymmetric gene flow, differential in N<sub>e</sub> along an upstream-downstream gradient, and upstream-directed colonization). The parameters of this model are resumed in Tab. 6.
Tab. 6: Description of the parameters considered for simulating genetic data under the dendritic theoretical model ruled by asymmetric gene flow, a differential of \( N_e \) along the upstream-downstream gradient and an upstream-directed colonization process.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>( M_{\text{DOWNSTREAM}} )</td>
<td>Downstream-directed migration rate</td>
</tr>
<tr>
<td>( M_{\text{UPSTREAM}} )</td>
<td>Upstream-directed migration rate</td>
</tr>
<tr>
<td>( P_{\text{ASYM}} )</td>
<td>Asymmetry rate = ( M_{\text{DOWNSTREAM}} / M_{\text{UPSTREAM}} )</td>
</tr>
<tr>
<td>( N_{\text{HEADWATER}} )</td>
<td>Size of the most upstream demes (effective number of diploid individuals)</td>
</tr>
<tr>
<td>( P_{\text{SCAL}} )</td>
<td>Scaling parameter for calculating downstream demes sizes with the recurrence relationship ( N_{n+1} = N_n \times P_{\text{SCAL}} ) (considering that ( N_0 = N_{\text{HEADWATER}} ))</td>
</tr>
<tr>
<td>( T_{\text{COLON}} )</td>
<td>Time elapsed between each colonization step (generations)</td>
</tr>
<tr>
<td>( T_{\text{END}} )</td>
<td>Time of the ending of the stepwise colonization (generations)</td>
</tr>
<tr>
<td>( P_{\text{FRAC}} )</td>
<td>Fraction of individuals colonizing a new deme</td>
</tr>
</tbody>
</table>

Then, we applied ABC parameter inference procedures considering the selected model to infer, for each species, the mean values for key dispersal parameters such as downstream-directed migration rates (\( M_{\text{DOWNSTREAM}} \)), upstream-directed migration rates (\( M_{\text{UPSTREAM}} \)) and dispersal asymmetry rates (\( P_{\text{ASYM}} \)) (Tab. 7).

Tab. 7: Mean parameters values inferred from the three-interacting processes model with ABC for each species. A non-linear regression correction method based on neural networks has been used to correct for the imperfect match between observed and simulated descriptive statistics (Csilléry et al. 2012). For the sake of clarity, we did not report in this document the results for the parameters related to the colonization process.

<table>
<thead>
<tr>
<th>Species</th>
<th>( M_{\text{DOWNSTREAM}} )</th>
<th>( M_{\text{UPSTREAM}} )</th>
<th>( P_{\text{ASYM}} )</th>
<th>( N_{\text{HEADWATER}} )</th>
<th>( P_{\text{SCAL}} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>\textit{Squalius cephalus}</td>
<td>0.109</td>
<td>0.095</td>
<td>1.149</td>
<td>300.509</td>
<td>1.215</td>
</tr>
<tr>
<td>\textit{Gobio occitaniae}</td>
<td>0.055</td>
<td>0.025</td>
<td>2.224</td>
<td>217.962</td>
<td>1.030</td>
</tr>
<tr>
<td>\textit{Barbatula barbatula}</td>
<td>0.079</td>
<td>0.058</td>
<td>1.363</td>
<td>140.550</td>
<td>1.215</td>
</tr>
<tr>
<td>\textit{Phoxinus phoxinus}</td>
<td>0.079</td>
<td>0.068</td>
<td>1.164</td>
<td>191.383</td>
<td>1.092</td>
</tr>
</tbody>
</table>
The results of this modelling approach show that the species that display the higher migration rates are *Squalius cephalus* and *Phoxinus phoxinus*. *Gobio occitaniae* displayed a non-negligible level of downstream-biased asymmetric gene flow, with a $M_{\text{DOWNSTREAM}}$ value two-times higher than $M_{\text{UPSTREAM}}$. Such a level of asymmetry may hence explain the pattern of IGDD observed for this species (see above). All the other species showed little differences between upstream- and downstream-directed migration rates, although in general downstream directed gene flow was higher than upstream-directed gene flow.

Overall, such a large spatial scale analysis reveals that the dispersal ability of these species is rather high, with all species being able to disperse among sites as far as dozens of kilometres. Interestingly, the upstream- and downstream-directed dispersal abilities of these species are similar, indicating that re-colonization processes may be bi-directional. However, such a type of dispersal makes sense over relatively large temporal scales (> ten generations), which is much longer than the timeframe of restoration plans. We therefore conducted an additional analysis at a shorter spatial scale (i.e. at the Célé river scale), by using inference methods that allow quantifying recent gene flow (that is, gene flow that occurred during the last two generations).

**Molecular estimates of dispersal on the Célé river using assignment methods.**

Molecular estimates of dispersal are based on the idea that individuals carry unique genotypes that are specific to the populations where they originated. Once these individuals leave their initial population to colonize new populations, these genotypes will be “introgressed” in the recipient populations. As such, these dispersal events leave “genetic footprints” in the recipient populations. Such genetic footprints can be used to (i) quantify the proportion of emigrants and immigrants in each sampled population, (ii) assign individuals to their original population and (iii) quantify the distance travelled by dispersers.

We here inferred these parameters from genetic data for two out of the four species presented below (*G. occitanae* and *P. phoxinus*) in the Célé river. For so doing, we used the ready-to-use program Geneclass2 (Piry 2004). This program implements different genetic assignment methods that are based on different assignment criteria computed for likelihood estimation (i.e. a genetic-distance criteria, a criterion based on allele frequencies and a Bayesian criteria; Paetkau *et al.* 1995; Rannala & Mountain 1997; Cornuet *et al.* 1999).

We thus applied the methods implemented in Geneclass2 to specifically characterize both downstream- and upstream-directed recent movements of individuals in the Célé River for the two fish species. We sampled individuals all along the river gradient (*Fig. 33*) so as to estimate the dispersal distances performed by the dispersers. For both species, up to 30 individuals were sampled for all sampling sites, and each specimen was genotyped for 15 microsatellite loci. The Geneclass2 analysis was performed for each species separately.
For the gudgeon, we identified 12 dispersal events that occurred in the last few generations (i.e. migration rate = 0.019), among which 6 were directed downstream and 6 were directed upstream (Fig. 34a). The mean distance travelled by specimens is around 10 km, although upstream-directed movements were strikingly lower in distance travelled (< 5 km) than downstream-directed movements (> 15km) (Fig. 34b). Accordingly, all very long-distance migration events were directed downstream (Figure 5a). Finally, it is noteworthy that both source (i.e. migrant donor) and sink (i.e. migrant receiver) populations tend to be in the upstream part of the river, since they are in average closer to the source than the mean of all sampling sites (Fig. 34c).
For the minnow, we identified 14 dispersal events that occurred in the last few generations (i.e. migration rate = 0.022), among which 8 were directed downstream and 6 were directed upstream (Fig. 35a). The mean distance travelled by specimens is around 12 km, although (as for the gudgeon) upstream-directed movements were strikingly lower in distance travelled (< 6 km) than downstream-directed movements (> 15km) (Fig. 35b). We however detected long-distance migration events that were directed both upstream and downstream (Figure 6a). Finally, source populations tend to be in the upstream part of the river whereas sink populations are, in average, at the same distance than the mean of all sampling sites (Fig. 35c).

To conclude, we obtained relevant information concerning the dispersal capacities of four freshwater fish species at different spatio-temporal scales. The description of spatial patterns of genetic diversity and differentiation of *Squalius cephalus*, *Gobio occitaniae*, *Barbatula barbatula* and *Phoxinus phoxinus* at the Garonne river basin scale shed light on their overall dispersal capacities at a large spatial scale and at an evolutionary time-scale (more than ten generations). Additionally, the combination of observed empirical data and data simulated under different competing dendritic meta-population models in a novel model-based inference framework allowed us to estimate dispersal parameters such as directional migration rates, as well as levels of asymmetry between downstream- and upstream-directed migration for each species at the river basin scale. Finally, we obtained via genetic assignment methods more precise estimations of directional migration rates, as well as estimates of dispersal distances, at a restricted spatial scale (i.e. the Célé river) and at a short, ecological time-scale (i.e. over the last two generations).
These results provide a strong comparison basis that nicely complements the outputs obtained with the GIS dispersal model and with the dispersal literature review. Indeed, contrary to physical measures of dispersal (e.g. CMR), genetic tools allow inferring dispersal parameters for individuals that efficiently participate to the receiving populations (i.e. that reproduce and provide progenies), which is essential from a restoration viewpoint. We hence believe that the work overviewed in this section will be valuable in the future for calibrating new models aiming at understanding how fish disperse in dendritic river networks, as well as for increasing our understanding on the genetic effects of dispersal on the distribution of genetic diversity of fish in freshwater ecosystems.

Fig. 35: (a) Graphical representation of the 14 dispersal events identified in the Célé River for *P. phoxinus*. Each event is symbolised by an arrow directed from the source population to the sink population. The number associated to certain arrows indicates the amount of dispersal events that occurred between these two sites when they were greater than one. (b) Mean distance (in km) of upstream-directed (black bars) and downstream-directed (white bars) movements. The dotted line indicates the averaged distance over all 12 events (the grey square indicates the 95 %CI). (c) Mean distance (in km) of source (black bars) and sink (white bars) populations from the river source. The dotted line indicates the averaged distance over all sampling events (the grey square indicates the 95 %CI).
3.7 DISPERsal MODEL FOR INVERTEBRATES (UDE)

Dispersal of a total number of 10 species was modelled using the Least-Cost-Modelling approach in the Treene catchment (section 2.3.1). For 10 species, the number of occurrences in the macroinvertebrate samples taken in the catchment was large enough to develop Species Distribution Models (SDMs) to predict source populations. Unfortunately, these 10 species did not overlap with the 8 species for which dose-response curves of the effect of nutrients were developed (section 3.5.2). Therefore, it was not possible to compare the effect of nutrients on the abundance and the re-colonization potential on macroinvertebrate species.

![Dispersal of Heptagenia sulphurea within the Treene catchment (conservative scenario). The area highlighted in grey displays the maximum dispersal extent within the catchment. The model reach is highlighted in red.](image)

The output of the dispersal model is a raster map displaying the maximum dispersal extent of a species for any of the three considered dispersal modes (aquatic upstream, aquatic downstream, aerial) within the catchment. Since most individuals of a distinct source population disperse over short distances while some disperse over long distances, two different models were run for each species, a conservative dispersal scenario (assuming low dispersal distances) and a progressive...
dispersal scenario (assuming high dispersal distances). The friction costs for each species to move through different aquatic and landscape features (Tab. 8) were assigned based on literature and expert judgment (for detailed information see Sondermann et al. 2014).

Tab. 8: Dispersal abilities (movement distance per life-cycle, usually one year for the 10 macroinvertebrate model species).

<table>
<thead>
<tr>
<th></th>
<th>Conservative scenario (Distance in m)</th>
<th>Progressive scenario (Distance in m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Upstream</td>
<td>Downstream</td>
</tr>
<tr>
<td>Anisus vortex</td>
<td>500</td>
<td>500</td>
</tr>
<tr>
<td>Brachycentrus subnubilus</td>
<td>50</td>
<td>100</td>
</tr>
<tr>
<td>Calopteryx splendens</td>
<td>30</td>
<td>50</td>
</tr>
<tr>
<td>Ephemerida danica</td>
<td>182</td>
<td>365</td>
</tr>
<tr>
<td>Kageronia fuscomigea</td>
<td>292</td>
<td>547</td>
</tr>
<tr>
<td>Heptagenia sulphurea</td>
<td>292</td>
<td>547</td>
</tr>
<tr>
<td>Lepidostoma hirtum</td>
<td>100</td>
<td>150</td>
</tr>
<tr>
<td>Orectochilus villosus Lv.</td>
<td>182</td>
<td>182</td>
</tr>
<tr>
<td>Paraleptophlebia submarginata</td>
<td>182</td>
<td>255</td>
</tr>
<tr>
<td>Serratella ignita</td>
<td>182</td>
<td>255</td>
</tr>
</tbody>
</table>

The re-colonization potential is given as percentage of the reachable amount of raster cells of the river network in the catchment, i.e. it was calculated by dividing the number of reachable raster cells by the total number of cells (for the river network).

Results of the conservative and progressive scenario are exemplarily shown for the species Heptagenia sulphurea (Fig. 36, Fig. 37). On the one hand, Least-Cost-Models were run based on source populations taken from the species distribution models, and actual findings from sampling data on the other hand. The prevalence (number of source populations) differs considerably between the two approaches. Dispersal models that are based on the actual findings of the model species within the catchment rely on few source populations only. The distribution of source populations is spatially restricted, covering only a small part of the whole river network. Accordingly, the number of source populations is underestimated since information about species occurrences is missing for the large parts of the river network. Dispersal models that are based on source populations generated by the species distribution models use a much higher number of source populations as input for the Least-Cost-Modelling. However, there is a high probability that not all source populations indicated by the species distribution models are colonized by the respective species. This leads to an overestimation of species occurrences within the catchment. Although both approaches most do not give an accurate estimation of the actual presence of the species, both approaches are nevertheless useful to evaluate the effect of the availability of source populations on the re-colonization potential in general.

Re-colonization potential for all species differed between model runs using source populations identified based on SDMs and sampling sites, respectively. In the conservative scenario, re-colonization potential based on SDMS was 4.1 - 34.0 percentage points higher compared to the model runs using sampling sites as source populations, as hypothesized above (Fig. 38). In the progressive scenario, differences were much lower with 1.1 - 20.9 percentage points (Fig. 39). Due to the lower differences in the progressive scenario, species-specific differences were similar, which resulted in a similar ranking of the species according to their re-colonization potential (Tab.
In contrast, the ranking of the species in the conservative scenario differed depending on which approach has been used to identify source populations.

A species-specific analysis revealed that in general, the maximum amount of reachable river sections differed clearly between species. For all merolimnic species, aerial dispersal was the most important dispersal mode, while aquatic dispersal contributed to a lesser extent to the overall distribution (Tab. 10). The amount of reachable river sections was increasing with maximum dispersal distance and number of source populations. Values were lowest for a conservative approach based on actual findings, whereas highest values were observed for the progressive scenario and source populations taken from the species distribution model.

In summary, it can be concluded that the re-colonization potential of macroinvertebrates was not strongly affected by the number of source populations in a progressive scenario but, similar to fish, highly depending on the number of source populations in a conservative scenario. The results showed, that along with the assumption of high dispersal distances (progressive scenario), differences in reachable river sections due to a higher number of source populations become less evident (Fig. 39) as opposed to the conservative scenario (Fig. 38). It can therefore be assumed,
that most parts of the river network can already be reached based on actual findings under the progressive model approach. Thus the consideration of additional source populations only leads to a slight increase in reachable rivers sections. For the conservative model approach we assumed much lower maximum distances. Consequently, many parts of the river network were not reachable in the first place. An increase in the number of source populations may therefore lead to a stronger increase of reachable river sections in general. Moreover, results indicated that the re-colonization potential most strongly depended on the scenario applied (conservative vs. progressive dispersal scenario), and hence, there is an urgent need for research on the dispersal abilities of macrorinvertebrates to reduce the uncertainty in the assessment of the friction costs and differences between conservative and progressive scenarios.

Tab. 9: Mean parameters: Ranking of the model species according to the percentage of the maximum reachable amount of river sections under different scenarios. C = Conservative scenario/Source populations from SDM, CR = Conservative scenario/Source populations from sampling data, P = Progressive scenario/Source populations from SDM, PR = Progressive scenario/Source populations from sampling data. Shortcodes for species are given in Table I.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>C (%)</th>
<th>CR (%)</th>
<th>Taxon</th>
<th>P (%)</th>
<th>Taxon</th>
<th>PR (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>AniVor</td>
<td>44</td>
<td>17</td>
<td>AniVor</td>
<td>90</td>
<td>AniVor</td>
<td>69</td>
</tr>
<tr>
<td>SerrIgn</td>
<td>37</td>
<td>16</td>
<td>LepiHirt</td>
<td>76</td>
<td>KageFusc</td>
<td>60</td>
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<tr>
<td>OrecVil</td>
<td>27</td>
<td>15</td>
<td>SerrIgn</td>
<td>70</td>
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<tr>
<td>LepiHirt</td>
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<td>14</td>
<td>CaloSple</td>
<td>64</td>
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<tr>
<td>CaloSple</td>
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<td>HeptSul</td>
<td>57</td>
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<td>EpheDan</td>
<td>24</td>
<td>12</td>
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<td>EpheDan</td>
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<tr>
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<td>OrecVil</td>
<td>48</td>
<td>BrachSub</td>
<td>38</td>
</tr>
<tr>
<td>HeptSul</td>
<td>21</td>
<td>9</td>
<td>OrecVil</td>
<td>43</td>
<td>OrecVil</td>
<td>38</td>
</tr>
<tr>
<td>ParaSub</td>
<td>18</td>
<td>6</td>
<td>ParaSub</td>
<td>34</td>
<td>ParaSub</td>
<td>29</td>
</tr>
</tbody>
</table>

Tab. 10: Re-colonization potential (percentage of the river network reachable) for the different scenarios, C = conservative scenario, P = progressive scenario, R = source populations based on sampling data, without R as suffix source populations based on species distribution models.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>CR Total</th>
<th>CR Air</th>
<th>CR Down</th>
<th>CR Up</th>
<th>C Total</th>
<th>C Air</th>
<th>C Down</th>
<th>C Up</th>
<th>PR Total</th>
<th>PR Air</th>
<th>PR Down</th>
<th>PR Up</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anisus vortex</td>
<td>10</td>
<td>na</td>
<td>5</td>
<td>5</td>
<td>44</td>
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<td>39</td>
<td>39</td>
<td>69</td>
<td>na</td>
<td>39</td>
<td>57</td>
</tr>
<tr>
<td>Brachycentrus subnubilis</td>
<td>12</td>
<td>12</td>
<td>1</td>
<td>0</td>
<td>21</td>
<td>21</td>
<td>17</td>
<td>17</td>
<td>38</td>
<td>38</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Calopteryx splendens</td>
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<td>6</td>
<td>1</td>
<td>0</td>
<td>25</td>
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<td>21</td>
<td>21</td>
<td>56</td>
<td>56</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Ephemera danica</td>
<td>14</td>
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<td>3</td>
<td>2</td>
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<td>24</td>
<td>15</td>
<td>14</td>
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Fig. 39: Comparison of the reachable amount of the river network within the Treene catchment for the progressive scenario. Source populations are based on the species distribution models (P) and on actual findings (PR).

Fig. 38: Comparison of the reachable amount of the river network within the Treene catchment for the conservative scenario. Source populations are based on the species distribution models (C) and on actual findings (CR).
3.8 INTERACTION MODEL

(CCMar)

As predicted, light and temperature had clear influence on both photosynthesis and respiration leading to higher respiration and photosynthesis rates (Fig. 40). However, only in the stones with algae habitat, the seasonal differences between GPP and respiration were evident (Fig. 41).

During summer, significant differences (p<0.05) in terms of GPP and respiration were detected between all habitats, except for gravel and leaf litter, which did not differ. During winter only stones with algae differed from the other habitats in terms of GPP, while in terms of respiration rates there was no statistically significant differences between habitats. Extrapolation of our results to the reach scale showed differences in terms of habitat cover, GPP and Respiration, with values during summer far exceeding those from winter season (Fig. 42).

The absence of differences among most habitats during winter demonstrates that environmental parameters (very high flow, low temperature) prevailed over biological processes during that season and impeded higher level structuring of different biological communities (Gasith, Resh 1999). During summer, with moderate discharge and high temperatures, differences in metabolism among habitats are more pronounced especially between highly productive and abundant stones with algae and other habitats. Extrapolating our results into reach scale demonstrated that filamentous algae contribute the most to the GPP and respiration values of the entire reach during summer and are mainly responsible for the large discrepancies in metabolism between two seasons. Rates of GPP during winter season are within a range of measured values for similar streams, however, during summer GPP of the habitat stones with algae was high when compared with analogous streams (Acuna et al. 2004). On the other hand respiration values for all the habitats were relatively low during both seasons, suggesting that autotrophic processes play far more important role in this ecosystem than heterotrophic processes.
Our preliminary results clearly showed the importance of seasonality and environmental parameters on habitat structuration and therefore river metabolism. Our next step will be to predict GPP and respiration as a function of (i) Environmental parameters (PAR, temperature, water flow) (ii) organisms responsible for observed differences in metabolic processes (chlorophyll a, biomass, macroinvertebrate biomass). To disentangle the effect of PAR and temperature we will perform some shaded incubations, to infer on the effect of riparian vegetation on metabolism. Additionally, nutrients samples before and after the incubation the will be collected in order to test how benthic organisms (algae, microorganisms, macroinvertebrates) associated with different types of habitat affect the water quality at different times of the year.

Fig. 41 Bubble plots representing the dependence of light (photosynthetic active radiation) and temperature on GPP and respiration for each habitat in two different seasons; The size of bubbles is proportional to the measured GPP and respiration values.
Fig. 42 The upper maps represent the situation from winter season in terms of habitat cover, GPP and Respiration (mg l^-1 h^-1), while the bottom maps represent situation in summer season.
3.9 FINAL BIOLOGICAL ASSESSMENT

(IGB, UDE, CAU)

For the final biological assessment, the modelling results on the habitat suitability and the re-colonization potential were combined in a semi-quantitative way (section 2.1).

The model species were ranked according to their re-colonization potential in the whole river network and the habitat suitability, i.e. they were classified as having a high or low probability to establish in the study reach (high or low habitat suitability) in the short or long term (high or low re-colonization potential) (Fig. 3, section 2.1). Relative values were used instead of absolute values for the following reason: For macroinvertebrates, the HET predicts the presence and abundance of specific species based on the habitat conditions. However, the absolute values on the Weighted Usable Area (WUA) given by conventional habitat models for fish, as well as the probability of occurrence given by the dispersal models cannot be directly transferred to species presence and abundance since the knowledge on the absolute values necessary to establish a population were missing. Furthermore, by quantifying the re-colonization potential in the whole river network, results were upscaled to assess the effect of restoring reaches in the river network to similar habitat conditions found in the near-natural study reach.

For fish, the re-colonization potential was quantified by calculating the species-specific share of the river network which was predicted to be reachable after three time-steps (years) using SDMs as source populations and including migration barriers (see section 3.6). In addition, the 95% confidence interval was calculated to consider the uncertainty of assessing the dispersal abilities (see equations for leptokurtic dispersal kernels section 2.3.2). The Weighted Usable Area (WUA) was standardized by calculating its share on the bankfull wetted area, which can be considered the maximum possible value, similar to the whole river network for the re-colonization potential. Besides using the median value of all 12 month, the range of the 12 values was calculated, with the minimum monthly value potentially acting as a bottleneck (for the reasons given in section 3.4. the WUA for Q50 was used).
In the near-natural study reach of the Treene river, habitat suitability did not differ much between the fish species for the present hydraulic habitat conditions (OK baseline scenario). Relative habitat suitability ranged from 40.7% to 63.7% for the 8 modelled fish species (median value of all 12 month), similar to the minimum monthly value which ranged from 30.6% to 43.1%. In contrast, fish species markedly differed in respect to the re-colonization potential, with a relative dispersal capacity of 27.4% to 88.3%. Therefore, it was concluded that the probability to establish in a restored reach given the habitat conditions will be similar for the modelled fish species but they markedly differ in the time needed for re-colonization. Habitat conditions worsen for most fish species due to the discharge changes caused by climate change (modelling period 2051-2060). Relative habitat suitability (median value of all 12 month) only slightly decreased (median for all 8 fish species -5.6 percentage points) but the minimum monthly value markedly decreased by -12.7

![Fig. 43 Comparison of the relative habitat suitability for fish (WUA related to bankfull wetted area) and relative dispersal capacity (share of reachable river network) for the Treene (left) and Célé (right).]
percentage points (median for all 8 fish species). There were no empirical data available and no information in literature to quantify the effect of such changes in habitat suitability on the presence or abundance of fish, but it seems reasonable to assume that such moderate changes of the bottleneck will probably have an effect on the abundance of the respective fish species but it is unlikely that abundance will dramatically decrease or locally get extinct. Therefore, restoration success could be affected by discharge changes caused by climate change but will not question restoration in general.

In the near-natural study reach of the Célé river, relative habitat suitability was generally lower compared to the Treene river, which was due to the shallower and wider cross-sections, resulting in a larger bankfull wetted area only partly inundated during median flow conditions (Q50). Similar to the Treene river, the present hydraulic habitat conditions (reference scenario) did not differ much between the modelled fish species. Relative habitat suitability ranged from 19.2% to 33.0% (median value of all 12 month) and from 8.0% to 21.7% for the minimum monthly value for the 11 fish species. In contrast, the re-colonization potential showed larger species-specific differences and ranged from 17.8% to 78.1%. These results indicated that the species-specific effect of restoration will be more dependent on the re-colonization potential than on the habitat needs of the species. In contrast to the Treene, habitat suitability was not predicted to decrease for all model species and some small-bodied fish potentially will benefit from the discharge changes (section 3.4.2). However, for these 3 fish species, the predicted increase in relative habitat suitability was only +2.2 (median value for all 12 month) and +3.5 (minimum monthly value) percentage points, respectively. For modelled fish species for which habitat suitability was predicted to decrease (n = 8), median and minimum monthly value dropped by only -2.1 and -1.0 percentage points (compared to -5.6 and -12.7 in the Treene study reach). Therefore, discharge changes due to climate change will probably have even a smaller effect compared to the Treene river and most likely will not affect restoration success.

For macroinvertebrates, the re-colonization potential was quantified by calculating the species-specific share of the river network which was predicted to be reachable after one life-cycle (one year for most model species) using SDMs as source populations (section 3.7). The range resulting from modelling the conservative and progressive scenario (section 3.7) were calculated and shown to consider the uncertainty of assessing the dispersal abilities. In contrast to fish, for which habitat suitability has been quantified using the Weighted Usable Area (WUA), the habitat model for invertebrates gives abundance values (section 2.3.2). In Fig. 44, the median and 10-90% percentile range of all abundance values modelled for the different substrate conditions (section 3.5.1) were shown.

In the near-natural study reach of the Treene river, the predicted abundance values of the model species differed even if the very drastic changes in substrate composition described in section 3.5.1 were assumed. Modelled abundance values for some species (e.g. 3 = Ephemera Danica, 1 = Brachycerentrus subnubilus) substantially differed for the different substrate compositions. Given that very dramatic changes in substrate conditions were included, which are unlikely to occur, these results indicated that discharge changes due to climate change will probably cause changes in the abundance of single species but no overall shift in the composition of the 7 model species. In contrast to fish, the re-colonization potential of the model invertebrate species was lower (18%-64% for invertebrates compared to 27.4%-88.3% for fish). Furthermore, modelling results did not show clear species-specific differences, which was due to the large differences between the conservative and progressive scenario resulting from the different assumptions on the dispersal abilities. These results stressed the need for empirical studies on the dispersal abilities of
invertebrate species to reduce the uncertainty in predicting the re-colonization potential. For the Célé study reach, no dispersal model was set up due to the missing data to develop species distribution models and hence, which did not allow for such a comparison of habitat suitability and re-colonization potential.

Fig. 44 Comparison of the predicted macroinvertebrate abundance for different substrate combinations (10-90% percentile shown as range) and relative dispersal capacity (share of reachable river network) for the Treene (1 = Brachycentrus submutilus, 2 = Calopteryx splendens, 3 = Ephemera Danica, 4 = Kageronia fuscogrisea, 5 = Heptagenia sulphurea, 6 = Orectochilus villosus Lv., 7 = Paraleptophlebia submarginata).
Discussion of Results

In this discussion section, a brief summary of the project will be given and results will be discussed. Furthermore, results will be compared to the initial objectives of the project.

The IMPACT project aimed at developing and testing an integrated modelling approach to predict the abiotic habitat conditions and to identify the main limiting pressures for biota in rivers for two organism groups: fish and macroinvertebrates (section 2.1). Besides modelling the abiotic habitat conditions, dispersal models were used to assess the species pool available for re-colonization of the habitats. The effect of a climate change scenario on discharge, resulting habitat conditions and biota was predicted in two case-study catchments, and in addition, the effect of climate change and land use change on nutrient pollution was modelled in one of the case-studies. Additionally, we inferred from genetic data relevant information concerning the dispersal capacities of four freshwater fish species at different spatio-temporal scales for one case-study catchment (i.e. Célé river). In each catchment, a near-natural study reach was selected as an analogue for the habitat conditions that can be expected to result from typical projects restoring natural channel dynamics at the reach-scale.

After developing the modelling framework (section 2.1), two novel modelling tools (section 2.3.2), and applying existing software tools (section 2.3.1), the modelling framework was tested in the two case-study catchments (section 2.2) (i) to assess the effect of discharge changes due to climate- and land-use scenarios (section 2.4) along the model chain of the ecohydrological (section 3.1), morphological (section 3.2), hydrodynamic (section 3.3), and habitat models (section 3.4, 3.5) on the habitat conditions and biota of the study reach, and (ii) to compare it to the effect of other pressures like nutrient pollution (section 3.5.2) and restricted (re-) colonization potential (section 3.6, 3.7), and assess to what extend large-scale pressures potentially constrain the effect of reach-scale restoration measures (section 3.9).

The ecohydrological model predicted a significant decrease of discharge in the Treene catchment in late summer and autumn (which was most pronounced in the last 10 years of the 2021-2060 modelling period), and in the Célé catchment in winter (especially for low-flow conditions). The effect of the land use scenarios on discharge was negligible, whereas nutrient concentrations slightly increased in one, and markedly decreased in two out of three land use scenarios. Since the ecohydrological model predicted only a slight decrease of the formative or channel-forming discharge in the Treene catchment, the morphological modelling results indicated that climate change will have a small or negligible effect on channel geometry, planform, and morphodynamics. The hydrodynamic model results reflected the decrease in discharge due to climate change and predicted a decrease in flow velocity, depth, and shear stress of up to 1/3 in the Treene study reach in late summer and autumn, and an even larger decrease in the Célé study reach where shear stress was predicted to half in winter. The habitat model for fish showed that the seasonal pattern of habitat suitability as well as the predicted effect of the hydraulic changes differed between large- and small-bodied fish. Moreover, the effect differed between species and depended on whether specific thresholds were passed. For some fish species, habitat suitability was predicted to decrease by up to about 4/5 in the Treene study reach in autumn (but starting from an already low level), while the mean decrease for all fish species was only about 1/10 and predicted habitat suitability in the Célé study reach in winter even increased for some species by
about 1/5. The habitat model for macroinvertebrates revealed that significant changes of the ecological status only resulted from drastic changes in substrate composition which is very unlikely to occur given the predicted discharge changes due to climate change. Furthermore, the predicted effect of changed nutrient levels in the land use scenarios differed between species, with both, negative and positive effects.

In the dispersal models for fish, the re-colonization potential markedly differed between species - a result that was supported by the genetic inference analyses - due to their dispersal abilities but the number and location of source populations was even more important. Furthermore, the number and location of source populations had a higher influence on the re-colonization potential compared to migration barriers in both case-study catchments. Although only based on two case-studies, these results indicated that considering potential source populations can have an even greater effect on the biological state and restoration success than restoring river continuity. Therefore, it is recommended that river management should focus on source populations which have not been adequately considered in the past, besides restoring river continuity. In the dispersal models for macroinvertebrates, the re-colonization potential also clearly differed between species, mainly due to the different dispersal modes of the species (aquatic, terrestrial, aerial). In contrast to fish, uncertainty in quantifying the dispersal abilities (movement distances) was high and even more strongly influenced the model outcome than the number and location of source populations. In the dispersal models, discharge and floods were not included as model parameters, and hence, discharge changes due to climate change did not affect the model results.

For the final biological assessment, habitat suitability and re-colonization potential was compared and visualized. In both case-study catchments, the hydraulic habitat conditions of the study reaches were similar suitable for all fish species and they more strongly differed in respect to the re-colonization potential. These results indicated that the species-specific effect of restoration will be highly dependent on the re-colonization potential given that the habitat needs of the species are generally met. Habitat suitability was generally predicted to decrease for fish in the Treene study reach due to discharge changes caused by climate change. However, even the minimum values which might act as a bottleneck decreased moderately, and hence it is unlikely that abundance will dramatically decrease or fish species locally get extinct. Therefore, the effect of restoration projects which result in similar habitat conditions compared to the near-natural study reaches will possibly be affected by discharge changes caused by climate change but climate change will not limit restoration success and question restoration in general. In the Célé study reach, the changes in habitat suitability were even smaller, and hence, climate change will probably not affect restoration success.

The preliminary results of the interaction model showed that biota potentially has a significant influence on water quality in the Quarteira study reach (final results are not reported here since funding and work was delayed by more than one year).

The final predicted effect of climate and land use change on biota was surprisingly low. It has to be noted that there are several habitat parameters which were not modelled in the two case-study catchments, which might be affected by climate and land use change, like fine sediment loads (since model performance was not sufficient), sediment sorting in general (since substrate in the Treene study reach consisted of pure sand), organic substrates like macrophytes (since respective models were missing), and temperature (since the project focused on discharge changes). Furthermore, only specific hydrological variables were considered (Q75, Q50, Q25), the assessment of the habitat suitability for fish was solely based on the hydraulic habitat conditions (as in most habitat suitability models), and on substrates and nutrient concentrations for the...
invertebrates, and transferability of the results is limited to catchments with similar catchment and river characteristics. Nevertheless, the results indicated that - given the above mentioned limitations and assumptions - the discharge changes caused by climate and land use change and the respective changes in nutrient loads will not necessarily have a strong effect on fish and invertebrates although a significant effect on discharge and the hydraulic habitat conditions was predicted.

In summary, the results showed that the modelling framework developed in the IMPACT project generally can be successfully applied to quantify the effect discharge changes caused by climate and land use changes on river morphology, hydraulics, and habitat conditions, to assess the effect on biota and to compare it to other pressures like water pollution or a low re-colonization potential. Furthermore, some more specific conclusions can be drawn from these first case-studies in respect to future model applications and research needs:

**Morphological model:** Since there was no physical-based morphodynamic model available to predict the dynamic equilibrium state and long-term evolution, the effect of discharge (changes) on different general aspects of channel morphology (channel geometry, planform, bathymetry) was modelled in three consecutive steps in the Treene study reach. Results indicated that changes of channel geometry, planform and morphodynamics will be small or even negligible, which was due to the small changes in bankfull discharge, which was used as a proxy for the channel-forming flow, and the highly cohesive banks stabilized by dense grassy vegetation. In contrast, significant changes of channel morphology and habitat conditions can be expected in rivers with less stable banks or larger changes of bankfull discharge, and hence, results did not imply that the morphological models can be neglected in the modelling framework. Furthermore, progress towards a physical model has been made recently (Asahi et al. 2013) and such models potentially could be used to model morphological changes in more detail, although practical applicability has to be tested.

**Hydrodynamic model:** Aquatic vegetation (macrophytes) affects channel flow, morphology and biota, especially in lowland rivers (Madsen et al. 2001, Suren and Riis 2010, Neary et al. 2010). Several studies investigated the habitat preferences of macrophytes at the reach scale (French and Chambers 1996, Riis and Bigggs 2003, Bornette and Puijalon 2011, O’Hare et al. 2011). However, the ability to predict macrophyte abundance and growth at the patch scale, which would be necessary to consider it in 2D hydrodynamic models, is still limited (Franklin et al. 2008). The results of the morphodynamic modelling in the Treene study reach indicated that macrophytes affected channel-bathymetry and stressed the need to develop tools to predict the presence, abundance, and growth of macrophytes.

**Habitat model for fish:** Due to the well-known opportunistic resources use and broad environmental tolerances of many species, fuzzy logic habitat suitability models are increasingly used (Ahmadi-Nedushan et al. 2006, Mouton et al. 2007) instead of habitat preference curves (Bovee et al. 1998). However, categorization of the habitat variables and assessment of the species-specific habitat suitability is mainly based on expert judgement, which might introduce observational bias especially for widely distributed species utilising a broad variety of waters and habitats. For example in one of the modelled fish species, classifications by several experts from different biogeographic regions resulted in significantly different model predictions of WUA (uncertainty analyses in preparation). Moreover, habitat suitability models are usually mainly based on hydraulic habitats (flow velocity and flow depth) and other habitat variables like substrate or channel features are often neglected. Therefore, there is an urgent need to derive empirically...
based rules for the fuzzy logic habitat suitability models and to include additional habitat parameters.

**Habitat model for macroinvertebrates:** The novel Habitat Evaluation Tool developed in the IMPACT projects allows to predict the presence and abundance of invertebrate species, which is not possible in conventional habitat models. The modelling is based on habitat-specific sampling data to derive empirical relationships between the presence of specific habitats and species abundance. Since mainly substrate-specific biological sampling data were available, application of the Habitat Evaluation Tool in the IMPACT project focused on substrate habitats but, in principle, other habitat parameters like hydraulic variables (e.g. flow velocity, flow depth, shear stress) could also be used. However, comparable and ecologically meaningful data on the hydraulic habitat conditions for a specific discharge (e.g. low, medium, high flow) are rarely available for biological sampling sites since flow measurements are restricted to the arbitrary discharge which occurred during field sampling. In a recent project, hydrodynamic models are used to predict the hydraulic habitat conditions for specific discharges at a larger number of biological sampling sites to develop such habitat-specific empirical relationships (GLANCE, Dr. Sonja Jähnig, IGB), which could be used in future applications of the Habitat Evaluation Tool.

**Dispersal models:** Developing FIDIMO was a major step forward in modelling the dispersal of fish. The first version of the model used in the IMPACT project predicts the probability of occurrence but the model can in principle be adapted to model fish individuals which, in combination with a module on fish reproduction and mortality, would allow to model the abundance of fish (instead of the probability of occurrence), spatially explicit population dynamics, and the establishment of new populations. The results showed that the uncertainty in quantifying the dispersal abilities of fish based on existing empirical data (literature review section 2.3.2) was low compared to the species-specific differences in the re-colonization potential (see error bars in Fig. 43). In contrast, the limited information available on the dispersal abilities of macroinvertebrates resulted in a high uncertainty of the modelling results which was larger than the species-specific differences and made interpretations difficult. These results stressed the need to derive information on the dispersal abilities of macroinvertebrates from empirical data to allow for a more robust modelling of the re-colonization potential.

Despite these specific limitations of some models and potential of improvement, the overall modelling framework is flexible and allows investigating different research and management options besides its application in climate change research: Additional pressures like water temperature increase or pollutants other than nutrients can be considered as additional input parameters in the habitat models. The effect of different restoration scenarios can be modelled, especially comparing measures which are implemented at different spatial scales like local reach-scale instream habitat measures, development of riparian buffer strips at the river network scale, and land use changes at the catchment scale.
5 Partners’ Involvement

As the SCP mid-term and final report is to be carried by the coordinator, this chapter aims at summarising each partner’s contribution to the project to give a general overview of the work undertaken by the project as a whole.

In the IMPACT project, five different partners from Germany, Portugal, and France were funded by the German Federal Ministry of Education and Research, the Portuguese Fundação para a Ciência e a Tecnologia, and the French National Agency for Water and Aquatic Environments (see cover page of report). In addition, two sub-contractors from the Netherlands were involved in the project and mainly worked on the 2D morphodynamic modelling (UU), and supervised the work of IGB on the meander migration modelling (IHE). Since partners were mainly responsible for specific models of the integrated modelling framework, the tasks were closely linked but it is also possible to clearly assign tasks to one single partner. In the previous sections of the report, the responsible partner was given below the heading using the abbreviations listed in Tab. 11. In case several partners were involved in a task, this was indicated by listing all partners ordered by their contribution.

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<td>UNESCO-IHE</td>
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</table>

Tab. 11: IMPACT project partners and abbreviations used.
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LAWA (2000). Gewässerstrukturgütebewertung in der Bundesrepublik Deutschland. Verfahren für kleine und mittelgroße Fließgewässer. Schwerin (Germany), Länderarbeitsgemeinschaft Wasser.


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# TERMS AND DEFINITIONS

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<td>BRT</td>
<td>Boosted Regression Trees: A statistical method to predict a response variable based on a set of predictor variables. A boosted regression tree model consists of a sequence of single regression trees, where each successive tree after the first one is built using the residuals of the preceding tree. The final BRT model is a linear combination of many trees that can be thought of as a regression model to predict the response variable where each term is a tree. BRT models were used in IMPACT to predict the presence of fish and macroinvertebrate source populations in the dispersal models (section 2.3.2, 3.5.1).</td>
</tr>
<tr>
<td>D&lt;sub&gt;50&lt;/sub&gt;</td>
<td>Median grain size of the channel-bed substrate</td>
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<tr>
<td>Delft3D</td>
<td>A 2D/3D hydro- and morphodynamic model used in IMPACT to model the effect of discharge changes on channel bathymetry (section 2.1).</td>
</tr>
<tr>
<td>FaSTMECH</td>
<td>A 2D hydrodynamic model used in IMPACT to predict the hydraulic habitat conditions (section 2.3.1).</td>
</tr>
<tr>
<td>FIDIMO</td>
<td>A fish dispersal model developed in the IMPACT project to predict the re-colonization potential of fish species based on their dispersal abilities, number and location of source populations, and migration barriers (section 2.3.2).</td>
</tr>
<tr>
<td>HEC-RAS</td>
<td>A 1D hydrodynamic model used in IMPACT to predict the water level at the downstream end of the study reaches for different discharges (section 2.3.1)</td>
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<tr>
<td>HET</td>
<td>Habitat evaluation tool: A new habitat model for macroinvertebrates developed in the IMPACT project which predicts the presence and abundance of species based on empirical data (calibration dataset on habitat-abundance relationships) and known or modelled habitat conditions (section 2.3.2).</td>
</tr>
<tr>
<td>MIANDRAS</td>
<td>A meander migration model which was used in IMPACT to assess the effect of discharge changes on channel planform and channel dynamics (section 2.3.1).</td>
</tr>
<tr>
<td>Q25, Q50, Q75</td>
<td>Discharge exceeded 25% 50%, and 75% of the days, i.e. the upper quantile, median and lower quantile of the flow duration curve. Used in IMPACT to describe the flow regime, i.e. high flow (Q25), median flow (Q50), and low flow (Q75) conditions (section 2.1).</td>
</tr>
<tr>
<td>SDM</td>
<td>Species Distribution Model: A statistical model to predict the presence of species based on environmental data like climatic or hydromorphological variables</td>
</tr>
<tr>
<td>STAR</td>
<td>STatistical Analogue Resampling Scheme: A method used by the Potsdam Institute for Climate Impact Research for the statistical downscaling of global climate change data which was used as climate change data for the Treene case-study catchment.</td>
</tr>
<tr>
<td>SWAT</td>
<td>Soil and Water Assessment Tool: A ecohydrological model used in IMPACT to model water quantity and quality (section 2.3.1)</td>
</tr>
<tr>
<td>WUA</td>
<td>Weighted Usable Area: Mean of the habitat suitability of all cells of a computational grid, weighted by the area of the grid cells. Describes the overall</td>
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habitat suitability of the study reach for a specific species and ranges from zero to the total modelled area (section 2.1).
## Glossary of Acronyms and Abbreviations

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<tr>
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<td>BRT</td>
<td>Boosted Regression Trees</td>
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<td>Delft3D</td>
<td>3D hydrodynamic model</td>
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<tr>
<td>FaSTMECH</td>
<td>2D hydrodynamic model</td>
</tr>
<tr>
<td>FIDIMO</td>
<td>Fish Dispersal Model</td>
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<tr>
<td>GIS</td>
<td>Geographic Information System</td>
</tr>
<tr>
<td>HEC-RAS</td>
<td>1D hydrodynamic model</td>
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<tr>
<td>HET</td>
<td>Habitat Evaluation Tool</td>
</tr>
<tr>
<td>IMPACT</td>
<td>Developing an integrated model to predict abiotic habitat conditions and biota of rivers for application in climate change research and water management</td>
</tr>
<tr>
<td>IPCC</td>
<td>Intergovernmental Panel on Climate Change</td>
</tr>
<tr>
<td>IWRM</td>
<td>Integrated water resource management</td>
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<td>MIANDRAS</td>
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<td>WFD</td>
<td>Water Framework Directive</td>
</tr>
<tr>
<td>WUA</td>
<td>Weighted Usable Area</td>
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