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SPECIAL ISSUE

Modelling of riverine ecosystems by integrating models: conceptual approach, a case study and research agenda

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ABSTRACT

Aim Highly complex interactions between the hydrosphere and biosphere, as well as multifactorial relationships, characterize the interconnecting role of streams and rivers between different elements of a landscape. Applying species distribution models (SDMs) in these ecosystems requires special attention because rivers are linear systems and their abiotic and biotic conditions are structured in a linear fashion with significant influences from upstream/downstream or lateral influences from adjacent areas. Our aim was to develop a modelling framework for benthic invertebrates in riverine ecosystems and to test our approach in a data-rich study catchment.

Location We present a case study of a 9-km section of the lowland Kielstau River located in northern Germany.

Methods We linked hydrological, hydraulic and species distribution models to predict the habitat suitability for the bivalve *Sphaerium corneum* in a riverine system. The results generated by the hydrological model served as inputs into the hydraulic model, which was used to simulate the resulting water levels, velocities and sediment discharge within the stream channel.

Results The ensemble model obtained good evaluation scores (area under the receiver operating characteristic curve 0.96; kappa 0.86; true skill statistic 0.95; sensitivity 86.14; specificity 85.75). Mean values for variables at the sampling sites were not significantly different from the values at the predicted distribution (Mann–Whitney *U*-test $P > 0.05$). High occurrence probabilities were predicted in the downstream half of the 9-km section of the Kielstau. The most important variable for the model was sediment discharge (contributing 40%), followed by water depth (30%), flow velocity (19%) and stream power (11%).

Main conclusions The hydrological and hydraulic models are able to produce predictors, acting at different spatial scales, which are known to influence riverine organisms; which, in turn, are used by the SDMs as input. Our case study yielded good results, which corresponded well with ecological knowledge about our study organism. Although this method is feasible for making projections of habitat suitability on a local scale (here: a reach in a small catchment), we discuss remaining challenges for future modelling approaches and large-scale applications.

Keywords

Benthic invertebrates, BIOMOD, Germany, HEC-RAS, hydraulics, hydrology, Kielstau, species distribution modelling, streams, SWAT.

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INTRODUCTION

Freshwater ecosystems, particularly rivers, are under severe pressure from multiple sources. Most rivers are in a state of progressive deterioration due to anthropogenic pollution, bank fixation, disengagement of floodplains or alterations in hydrology, resulting in severe loss of aquatic and riparian biodiversity. Additionally, they are among those ecosystems most severely affected by climate change (Vörösmarty *et al.*, 2010). To avert further decline in the health of aquatic ecosystems, measures for sustainable use should be implemented. Such measures could be based on integrated models that deliver a sound understanding of ecosystem functions, their interactions and feedback mechanisms across different spatial and temporal scales. However, the highly complex interactions between the hydrosphere and biosphere, as well as multifactorial relationships, are a challenge to represent in models, with first attempts focusing on the terrestrial phase (Weber *et al.*, 2001; Fohrer *et al.*, 2002), on pollutants connected to agricultural activities (Pohlert *et al.*, 2005; Lam *et al.*, 2010) or the transport of pesticides (Holvoet *et al.*, 2007; Dietrich *et al.*, 2011). Ecological models predict, for example, the occurrence of aquatic organisms in relation to land use or anthropogenic stressors, provide approaches to assess the effects of spatial processes across various scales or take into account management options (Statzner & Borchardt, 1994; Harby *et al.*, 2004; Adriaenssens *et al.*, 2007; Goethals *et al.*, 2007). Biotic aspects are included less often in integrated modelling studies (but see Statzner & Borchardt, 1994; Dedecker *et al.*, 2004; Holguin & Goethals, 2010).

These models are often set for particular river systems or river segments (Bovee *et al.*, 1998), but for the evaluation of the impacts of climate and/or land-use changes on aquatic ecosystems at larger scales there is still a lack of models that are capable of fully describing links within the environment and between the environment and the organisms within it (Kiesel *et al.*, 2009). Species distribution models (SDMs) are useful for predicting ecological responses to changing environmental conditions that can be applied to any scale, provided that suitable predictors are available (Elith & Leathwick, 2009). They are more commonly applied to terrestrial organisms and have proven to be valuable tools in the context of vegetation ecology and conservation management. In streams, large-scale and predictive modelling, as applied in climate change impact studies, is limited (e.g. Castella *et al.*, 2001; Statzner *et al.*, 2008), but recent modelling studies have embraced extensive regions of riverine environments, especially for fish and invertebrates (Domínguez-Domínguez *et al.*, 2006; Buisson *et al.*, 2008; Depraz *et al.*, 2008; Cordellier & Pfenninger, 2009; Mouton *et al.*, 2010; Balint *et al.*, 2011; Domisch *et al.*, 2011).

We consider benthic invertebrates to be ideal as a study group; they live on and within the substrate of the river bottom (the benthos), and comprise numerous groups such as crustaceans, molluscs, worms, turbellaria and insects. The occurrence of benthic communities is dependent on the characteristics of the catchment and on suitable aquatic habitats being available at the section or site scale (Molnar *et al.*, 2002; Kiesel *et al.*, 2010a). Relevant catchment parameters include seasonal discharge patterns, flood frequency, elevation, geology or land use (Vinson & Hawkins, 1998; Kiesel *et al.*, 2009). Hydromorphological conditions are the controlling factors on a reach scale, including stream width, substrate roughness or riparian land use, longitudinal (along the upstream–downstream axis of the river, e.g. blockage by weirs or dams), lateral (characteristics of the riverbanks, the extent of the functioning floodplain and riparian habitats) and vertical continuity (connection to the hyporheic zone and the groundwater) (Brosse *et al.*, 2003; Arscott *et al.*, 2005; Boulton, 2007). On the site scale, relevant habitat parameters include shear stress, water depth, substrate, sediment stability, shading and physicochemical water parameters (Allen & Vaughn, 2010). Riverine ecosystems and their benthic invertebrate communities are thus shaped by a wide variety of processes and conditions, which render them very heterogeneous, even on a local scale.

Our general aim was the development of a suitable integrated modelling framework for benthic invertebrates that takes this complexity into account. As mentioned, there are other modelling approaches available, but our integrated method differs in that it allows for full control of the design and linkage of the models, especially related to hydrological and hydraulic modelling in ungauged catchments (Caspar *et al.*, 2011); performs sensitivity analysis for the separate models; pursues an ensemble approach to account for different model outcomes and uncertainty; and most importantly is capable of upscaling in space and time. Although not all these advantages have been implemented so far, we can present a case study of our approach in a data-rich study catchment.

MATERIALS AND METHODS

General approach

The integrated modelling technique developed uses different models to provide the environmental data and to describe the relationship between organisms and the environment. The modelling approach considers the hierarchy of environmental variables at different scales in river ecosystems. It links the catchment to in-stream processes and then to the biota by following the driver–pressure–state–impact (DPSI) framework (Fig. 1). The modelling system can potentially analyse changes of climate, land use and river morphology and their effects on the hydrosphere, in-stream processes and aquatic habitats down to ecosystem responses. It facilitates the evaluation of both landscape and in-stream measures aimed to improve aquatic habitats.

The model system consists of the ecohydrological Soil and Water Assessment Tool 2005 (SWAT; Arnold *et al.*, 1998), the one-dimensional hydraulic model Hydraulic Engineering Center – River Analysis System 4.1.0 (HEC-RAS; USACE, 2010) and SDMs as provided in the package BIOMOD 1.1–6.9 in R (Thuiller *et al.*, 2009; R Development Core Team, 2011).

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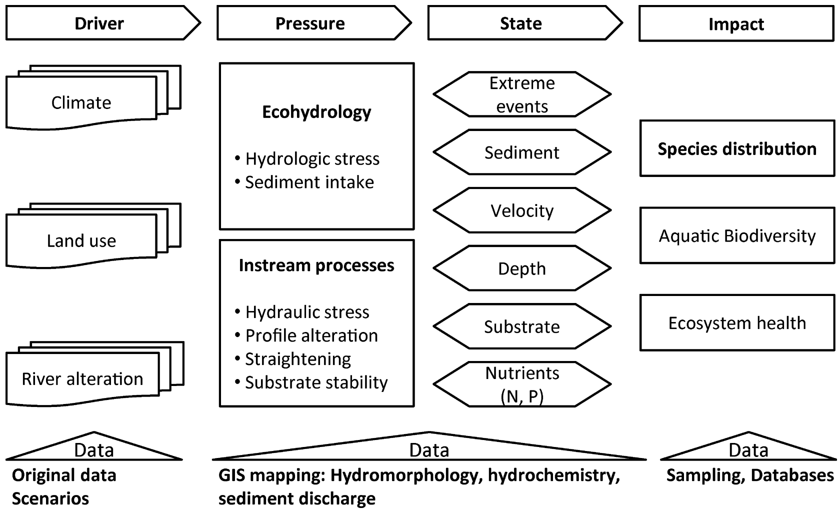

Figure 1 Integrated approach to modelling aquatic ecosystems following the driver–pressure–state–impact (DPSI) concept. (1) Major drivers are used as the model input data and are depicted by jointly considering stream and catchment processes. (2) The main pressures on the aquatic ecosystem are defined and represented in the model algorithms. (3) Based on the multiple pressures, it is possible to dynamically assess changes in the states of habitat parameters in the model output. (4) Finally, the impacts of the states on the aquatic ecosystems can be evaluated, closing the complex cause–effect chain from the drivers to the impact. Grey shaded cells highlight model domains.

Integrated model environments according to this methodology are currently being developed in three German catchments, namely the Kielstau (50 km²; Kiesel *et al.*, 2009, 2010a), the upper Treene (530 km^2; Guse & Fohrer, 2011) and the Kinzig [a site of the Long Term Ecological Research Network (LTER), 1500 km^2; B.S. *et al.*, unpublished data], and in the southern Chinese catchment of the Changjiang (1700 km^2; Kuemmerlen *et al.*, 2012; Schmalz *et al.*, 2012), each covering different key aspects. Further advancement is planned by realizing a hydrology-based model system with European spatial coverage, based on the WaterGAP Global Hydrology Model (WGHM) by Döll *et al.* (2009). Of these studies, the Kielstau catchment, which serves as a UNESCO demonstration site for ecohydrology, has a very good database and is the most advanced in terms of model integration (Schmalz & Fohrer, 2010). It is thus presented below as a case study, with the example of predicting a suitable habitat area for the bivalve *Sphaerium corneum* (Linnaeus, 1758), the European fingernail clam.

The Kielstau subcatchment has an approximate area of 50 km² and is located in the northern German lowlands (Fig. 2). The Kielstau Stream is one of the headstreams of the Treene River, which is part of the Eider catchment. The integrated modelling approach was applied to the 9-km section of the Kielstau Stream, downstream of Lake Winderatt.

Models and integration steps

Hydrological models

Abiotic environmental properties on the catchment scale are known to affect riverine communities (Quinn & Hickey, 1990). Hydrological models use these properties as input data to simulate the hydrological cycle and can, for example, depict run-off from a watershed, calculate the nutrient loads (Horn *et al.*, 2004; Hörmann *et al.*, 2005) or predict droughts or floods. They are based on equations describing the hydrological cycle both in space and time and can thus give a detailed description of the hydrological processes in the catchment. Furthermore, they are used for evaluation, planning and simulating the implementation of management measures, such as the improvement in water quality at the watershed level (Lam *et al.*, 2010, 2011). The effects of climate or land-use change on the watershed responses can be predicted; thus, these models are useful for environmental impact assessment studies (Fohrer *et al.*, 2005) or for integrated water management (Singh & Woolhiser, 2002).

The joint application of hydraulic and biological models requires hydrological information on specific locations, such as stream sections or species occurrence points; for this purpose, a (semi-)distributed, physically based hydrological model is required. In such a distributed model, the spatial variation of input parameters and variables is considered, and the watershed is divided into spatially distinct areas of similar physical conditions.

SWAT is a physically based, semi-distributed model and has been proven to produce reliable results in various studies for integrated water management and has gained international acceptance as a robust interdisciplinary watershed-modelling tool (Arnold & Fohrer, 2005; Gassman *et al.*, 2007; Kiesel *et al.*, 2010b; Lam *et al.*, 2011). It can simulate water balance, nutrients and pesticides, erosion, plant growth cycles, management practices and water bodies on a daily time-step for continuous simulations over long time periods using spatially distributed data on GIS maps, climate data and physical information from a relational database. Inputs

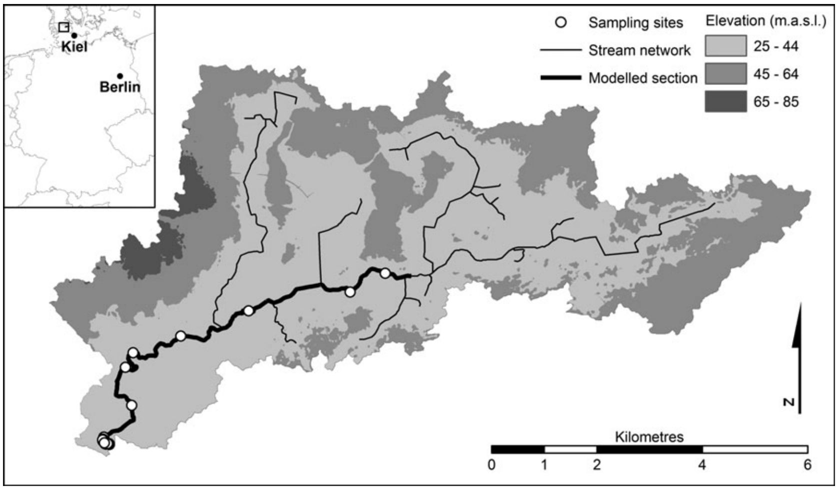

Figure 2 The study location in the Kielstau catchment in northern Germany, with the modelled stream section shown in bold (map according to LVA, 2008).

include spatial information, such as topography, soil and land-use data; additionally, management inputs include crop rotations, tillage operations, planting and harvest dates, irrigation, fertilizer use and pesticide application rates. Climatic variables are required for simulating water flow, sediment transport, crop growth and nutrient cycling (see Neitsch *et al.*, 2005 for details). It links the advantages of being an integrated model (e.g. describing the water balance and water-coupled fluxes of matter) and being applicable in a wide spatial range (i.e. from small to very large watersheds).

The first step in the integration process is to obtain water and sediment fluxes for the Kielstau catchment from the SWAT model (Fig. 3). Evaporation is simulated with the Penman–Monteith equation, surface runoff with the Soil Conservation Service (SCS) curve number method, interflow with a kinematic storage model and baseflow is calculated through the water balance of two groundwater aquifers.

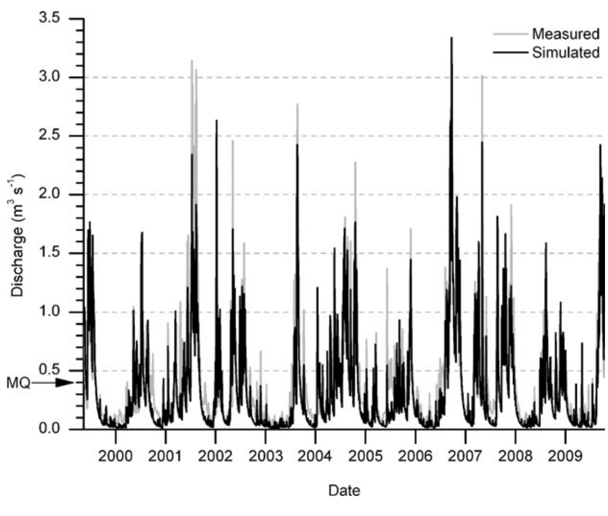

Figure 3 Measured (grey) and simulated (black) Soil and Water Assessment Tool (SWAT) discharge line. Variables to be derived could include the mean discharge (MQ, as indicated by the arrow), maximum/minimum discharge in a defined period or mean seasonal flow values.

Channel flow values are obtained by routing the received water with a variable storage coefficient method. The modified universal soil loss equation (MUSLE; Williams, 1995) is utilized to simulate field erosion. ArcSWAT (Winchell *et al.*, 2007) is used to prepare the input files from land use (DLR, 1995), soil (BGR, 1999; LANU, 2006), topographic (LVA, 1992–2004) and climate (DWD, 2009) data in ArcGIS 9.2 (http://www.esri.com/). The model setup, application and performance are explained in detail in Kiesel *et al.* (2010b).

Hydraulic models

At reach-scale to site-scale the organisms are affected by in-stream qualities such as flow velocity, depth or substrate size and type (Vinson & Hawkins, 1998); thus hydraulic models are required to describe these parameters. Hydraulic models combine the morphological conditions of the river reach with discharge ranges into a set of hydraulic parameters that are of major importance to the physical appearance of the aquatic habitat (Steuer *et al.*, 2008). Furthermore, fine sediment delivery to, and storage in, stream channel reaches can be considered as it may disrupt aquatic habitats, affect river hydromorphology and transfer adsorbed nutrients and pollutants from catchment slopes to the fluvial system (Jarrit and Lawrence, 2007). Models for simulating open channel flows can depict these variables both temporally and spatially. In general, one-dimensional (depth and width averaged) or two-dimensional (depth averaged) simulation codes are applied in aquatic habitat modelling (Harby *et al.*, 2004). Besides flow velocity, depth or sediment discharge, state-of-the-art hydraulic modelling systems describe substrate conditions (USACE, 2010; Berger *et al.*, 2011), which are important factors for species occurrence (e.g. Hauer *et al.*, 2011). However, applications in which substrate properties are simulated continuously for years are rare: the reasons for this are the difficult validation, substantial input data requirements and high computational demand.

The results from the hydrological SWAT model serve as input for the hydraulic HEC-RAS model, which simulates one-dimensional open channel hydraulics and sediment transport processes in river networks. It contains a number of sediment transport formulae to calculate in-stream sedimentation and erosion, and can perform steady flow, unsteady flow, sediment transport/mobile bed computations, water temperature modelling and water quality analysis (USACE, 2010). It utilizes the momentum equation in the case of supercritical flow and on hydraulic structures, and solves the energy equation for basic profile calculations with the standard step method. HEC-GeoRAS (USACE, 2005) is used to prepare HEC-RAS input files from river geometry (soil-AQUA, 2009) and morphology data (DAV-WBV/LAND, 2006) in ArcGIS.

An ArcGIS interface is used to couple SWAT and HEC-RAS (Kiesel *et al.*, 2012). Flows and sediment loads from each SWAT tributary are transferred to the respective HEC-RAS cross-sections for each daily time step. Hydraulic and substrate-specific parameters were extracted from HEC-RAS at the 544 cross-sections along the 9-km-long river section from 2006 to 2009, and annual mean values were calculated based on daily parameters. All HEC-RAS cross-sections were then linearly interpolated to obtain a total of 1590 continuous hydraulic parameter ASCII maps with a 5-m grid size (1730 cells), which were then used to select the appropriate predictors for SDMs.

Species distribution models

biomod is used for modelling the geographic distributions of species and their environmental requirements. Occurrence data are statistically correlated with environmental data at each site to describe an environmental niche. Distributions are later projected to other areas where similar suitable conditions are found, and occurrence probabilities are computed. The modelling procedure within biomod employs several individual algorithms, and provides an ensemble forecasting to reduce uncertainties in predictions derived from different modelling algorithms (Thuiller *et al.*, 2009).

An ensemble model was created for *Sphaerium corneum*, based on a generalized linear model (GLM), a generalized additive model (GAM) and a generalized boosting model (GBM) at a spatial resolution of 5 m. Occurrence data were derived from the following unpublished surveys conducted between 2002 and 2010: a 2002 survey by R. Brinkmann, Schlesen, Germany (freelance biologist; contact details available from S.C.J.); a 2006 survey by the Schleswig-Holstein State Agency for Nature and Environment (LANU), Flintbek; 2008 and 2009 surveys by M. Stengert *et al.*, University of Duisburg-Essen, Germany; and a 2002/2003 survey by the Schleswig-Holstein State Agency for Agriculture, Environment and Rural Areas (LLUR), Flintbek. Clam occurrence data at 34 known occurrence locations were split into a training set (70%) and a testing set (30%) by applying a random partition as described in Araújo *et al.* (2005), which allows a validation analysis to be performed based on one occurrence data set. Each algorithm used 500 pseudo-absences, following the recommendation of Barbet-Massin *et al.* (2012) to use a relatively large number of pseudo-absences and 10-fold cross-validation for model calibration, resulting in a total of 34 models including consensus models. Because of the small size of the case study catchment and the available number and distribution of sampling data for organisms, we used a hydraulically oriented subset of available data, omitting data on hydrology, water quality, temperature or land use from an original set of 20 variables by pairwise correlations ($-0.7 < r < 0.7$) and expert knowledge. However, some variables, for example land use, are still indirectly considered via the implementation in the SWAT model. Four environmental predictors were used for each grid cell: water depth (m), flow velocity (m s^{-1}), stream power (kg m^{-1} s^{-1}) and sediment discharge (metric tonne day^{-1}). The variable 'stream power' represents the energy dissipation against the streambed and banks, a combination of shear stress and velocity, while the variable 'sediment discharge' measures the transport of sediment. Because organism data were spatially and temporally heterogeneous, we decided to use annual means for each grid cell. The final model results from a weighted average consensus procedure to minimize uncertainties derived from different algorithms, known as an ensemble model. For this purpose single algorithm results (10 repetitions per algorithm) were averaged by multiplying their AUC (area under the receiver operating characteristic curve) scores with a decay weight of 1.6. The use of weighted averages has been proven to be superior in creating consensus models (Marmion *et al.*, 2009). We finally transformed the model output into a binary presence–absence map by applying a cut-off value which minimizes the difference between sensitivity and specificity (Liu *et al.*, 2005). We extracted the ranges of the modelled variables at the sampling sites to describe the preferred habitat and compared them with variable values at the modelled sites. The contribution of each variable in the final ensemble model was assessed by giving each variable used by the GLM, GAM and GBM the same weighting factor that was used for building the consensus projection.

RESULTS

The SWAT model showed a good model performance (root mean square error, RMSE = 0.06, r^2 = 0.82, Nash–Sutcliffe efficiency, NSE = 0.78; for details see Kiesel *et al.*, 2010b). Likewise, the linked SWAT–HEC-RAS model simulates the hydrological and hydraulic regime from 2006 to 2009 in very good agreement with measured data (Fig. 4a,b). Sediment simulations were validated with suspended sediment measurements, leading to an agreement in monthly sediment loads of r^2 = 0.68 (data not shown).

Sphaerium corneum is predicted to occur in 232 raster cells according to our results, i.e. in about 13.4% of the modelled area. The ensemble model (Fig. 5) obtained good evaluation scores (AUC 0.96; kappa 0.86; true skill statistic, TSS, 0.95; sensitivity 86.14; specificity 85.75). Mean values for the modelled variables at the sampling sites of *S. corneum* are very

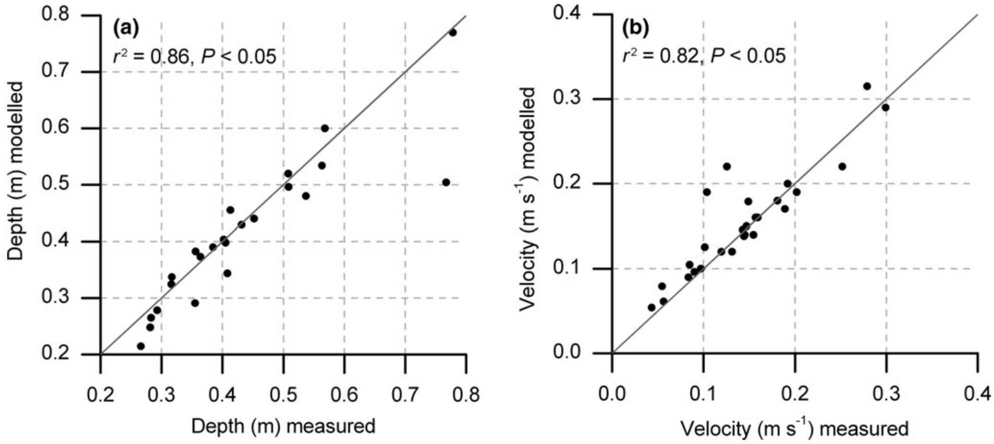

Figure 4 Hydraulic Engineering Center – River Analysis System (HEC-RAS) model values and comparison to measured values (F. Tavares & J.K., unpublished data) for depth (a) and velocity (b). The grey line represents a 1:1 line. Variables to be derived could include the mean or maximum/minimum parameter values for a defined period of time.

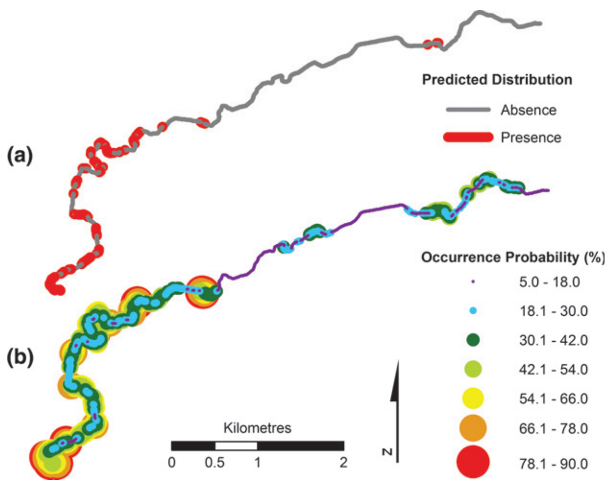

Figure 5 Predictions of *Sphaerium corneum* as (a) presence/absence and (b) occurrence probabilities along the modelled 9-km section of the Kielstau Stream.

similar to the values of the predicted distribution (Table 1; Mann–Whitney *U*-test not significant for all variables, $P > 0.05$). High occurrence probabilities were predicted in the downstream half of the 9-km section of the Kielstau. The most important variable for the model was sediment discharge, contributing 40%, followed by water depth (30%), flow velocity (19%) and stream power (11%).

DISCUSSION

Integrated modelling of *Sphaerium corneum* in the Kielstau catchment

To model invertebrate occurrences in a catchment framework, actual flow and sediment boundary conditions of the hydraulic modelling domain have to be known for all tributaries during the entire modelling period. This dynamic link poses a challenge for modelling and was solved by using a hydrological model to depict flow and sediment contributions. These data, influenced by catchment management practices and the natural climate, serve as inputs into the hydraulic model: this is then used to simulate the resulting water levels, velocities and sediment processes depending on stream channel characteristics. By considering these abiotic parameters, a major part of the functional chain influencing the occurrence of *S. corneum* can be depicted.

The results in this case study correspond to the known basic ecological requirements of *S. corneum*, which has been described from a range of habitats, from wells below springs (metarhithral) to lentic sites and ponds (littoral) (Nesemann & Reischütz, 2002; Schmidt-Kloiber, 2011). It is plausible that a freshwater clam such as *S. corneum* is dependent on slowly flowing water for the provision of organic sediment to filter and feed upon. A strong current would either erode the fine sediment it burrows in or may even dislodge the clam and transport it downstream. A certain depth in the water column is necessary to withstand temporal fluctuations of the river discharge (Dussart, 1979). In this model, predictions of occurrence seem to cluster at river bends, where sediment discharge, flow velocity and stream power tend to be reduced, while water depth tends to increase in contrast to straight sections. In this small-scale case study, the data produced proved to be sufficient to successfully model the distribution of *S. corneum*.

Challenges and outlook: integrated modelling of river ecosystems

Species distribution models of aquatic invertebrates have not been used extensively for large-scale analysis, despite promising first attempts (Balint *et al.*, 2011; Domisch *et al.*, 2011). Typically SDMs rely on terrestrial-based bioclimatic data. However, the abiotic factors that structure riverine communities are different from those that influence communities in the terrestrial realm. These particular factors in

Table 1 Mean values of the modelled variables at the riverine sampling sites and the predicted occurrence of *Sphaerium corneum*, and variable ranges in the whole 9-km study area along the Kielstau River (min.–max.). Mann–Whitney *U*-test between grids of sampling sites and predicted occurrence was non-significant ($P > 0.05$) for all variables.

	Sampling sites (± SD)	Predicted occurrence (± SD)	Study area
Sediment discharge (metric tonne day^{-1})	2.64 (± 1.55)	2.96 (± 1.92)	0.07–19.12
Water depth (m)	0.29 (± 0.04)	0.29 (± 0.04)	0.11–0.51
Flow velocity (m s^{-1})	0.21 (± 0.05)	0.22 (± 0.06)	0.04–0.95
Stream power (kg m^{-1} s^{-1})	0.81 (± 1.12)	1.01 (± 1.58)	0–67.28

riverine ecosystems call for integrated modelling approaches to provide habitat suitability predictions of aquatic organisms using adequate predictors.

Several challenges related to the particular environmental conditions in rivers remain, and a full model for riverine invertebrates would have to include the following variables and dependences:

1. Hydrological time series are required to derive the low and high flow extent and dates or other seasonally dependent variables. The correct depiction of peak and low flows for single events can be very exact when using small modelling time steps with sufficient data. However, over long time periods, the depiction of extremes lacks accuracy due to data constraints because topography, artificial drainage pathways, soils and land-use data are usually not available dynamically. Sediment and water quality modelling inherits high uncertainties; thus, the reliable generation of such output from a hydrological model in ungauged basins is still a challenge.

2. A full model should also include variables related to hydraulic conditions on the reach or site scales, such as shear stress, sediment availability or distribution, current velocity, water depth and river bed morphology (e.g. riffle-pool sections, shoreline shape and other similar variables). For hydraulic models, modelling sediment transport and substrate changes on local scales with reasonably small error margins is a challenge due to the availability of temporal, spatial and physical substrate data and computation time.

3. Other abiotic predictors in stream environments that are not provided by hydrological/hydraulic models have either scarce data or data that are collected independently from biological data, and it is not always easy to combine these. Such data include, for example, stream temperature, oxygen content and nutrient availability, the latter two both being dependent on the first: temperature. Although stream temperatures may be estimated from air temperatures (Caissie, 2006), this imposes the challenge of including factors that are directly and indirectly linked to the stream and that affect stream temperature patterns, e.g. riparian vegetation, geography and urban settlement (Caissie, 2006). Furthermore, it is important to bear in mind that water provides a buffering solution, and that the lotic state causes a spatial (by the linear structure) and hence temporal lag compared to the outside.

4. Catchment-related variables, including riverine vegetation and different land-use types (most prominent is the proportion of urban land use), are rather easy to obtain. Additionally, in many parts of the world virtually all rivers show impact from past anthropogenic influence. This 'ghost of land use past' (Harding *et al.*, 1998) is considered one of the major predictors for current communities, but is rarely considered in an adequate way in either ecological studies or modelling approaches. Eventually, it is unclear how significant influences from upstream areas or certain lateral influences from directly adjacent areas (Kail & Hering, 2009; Kappes *et al.*, 2011) could be considered in stream SDMs.

5. While for some issues an improved database might help (e.g. stream temperatures, nutrients, past and current land-use data, etc.), other challenges may be addressed by integrating further models, either directly or by coupling of model output. For instance, coupling a vegetation model (Hickler *et al.*, 2004) with a hydrological model could further improve data accuracy in terms of temperature predictions, shading or organic material input. Guisan & Thuiller (2005), Elith & Leathwick (2009) or Schurr *et al.* (2012) mention that there are attempts to integrate SDMs with dynamic and other kinds of models to better represent ecological processes and to allow the inclusion of mechanistic, population and landscape change effects, but none of these attempts consider riverine ecosystems.

6. In addition to abiotic drivers, biotic factors also restrict the availability of suitable habitat for species. One special challenge is posed by the different life stages of stream macroinvertebrates. Insects have different larval and adult live stages, which should be considered differently in the models, by life-stage-specific habitat requirements or even more pronounced when aquatic and terrestrial life stages are passed. A classic full dispersal assumption, which is often applied, probably falls short when considering major relevant barriers to both aquatic life stages (dams) or aerial life stages (land use, light pollution).

7. In addition, several of the aquatic organism groups show large natural dynamism (e.g. macrophyte growth and subsequent ecological effects). They might also show highly complex behaviour, such as migration, compensation flights or drift, which are not fully understood and thus are difficult to consider in a model. Because of the linear structure and lateral influences, communities are highly dependent on distance, size and conditions of source populations in the surroundings or remaining catchment (Brederveld *et al.*, 2011). Interactions between organisms themselves are not yet taken into account; however, this is a problem shared by most biotic models. To develop a common concept of how barriers, source populations and interactions could be considered in a SDM would set a new benchmark for niche modelling, and approaches are being presented by Kissling *et al.* (2012), Marion *et al.* (2012) and Schurr *et al.* (2012).

8. Similar to other SDM applications, the 'presence–absence challenge' is still unsolved, and it seems that dispensing with pseudo-absences is particularly tricky in river ecosystems. An absence at a river sampling site might be caused by different processes, including true absence, seasonal absence (aquatic/terrestrial life stage), the rather obscure sampling habitat for humans, the short-term removal of organisms by flood or other drift-causing events. The help of an observational model (Marion *et al.*, 2012) could assist in overcoming the use of pseudo-absences.

CONCLUSIONS

From this and other studies (Kuemmerlen *et al.*, 2012; Schmalz *et al.*, 2012), we conclude that the proposed model integration between hydrological, hydraulic and species distribution models is a feasible approach to gain further insights into the distributions of stream organisms. The presented model approach is in principle transferable to other catchments or taxa of interest. Yet we acknowledge the shortcomings of our approach: it is data intense by, for example, requiring hydrological and hydraulic models to be elaborated beforehand for a specific catchment or region, and requires extended biological datasets and relevant abiotic data. Furthermore, several challenges remain for future modelling approaches, such as the difficulties that arise from considering the environmental parameters required in continental to global studies (i.e. large-scale studies).

One of the most evident advantages of our approach is the use of public domain (open source) models at all levels, control of input data in models and the linkages between them, hence the chance to improve calibration and projections of different spatial and temporal scales within riverine environments, and the use of (biological) ensemble models to allow for uncertainty analysis. Such models can provide useful information for environmental management of the stream channel or the landscape. If there is sufficient knowledge of a catchment, predictions could be made of, for example, how planned changes in land use might alter the composition of the community in a stream. Furthermore, response curves might be useful for selecting indicator taxa (Dedecker *et al.*, 2004) or determining the most influential environmental variables for communities.

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BIOSKETCH

Sonja C. Jähnig is a stream ecologist who is interested in the combination of different models to predict the impact of climate change on stream ecosystems. She focuses on stream benthic invertebrates. Her research is based on SDMs at different spatial scales, which are constantly being improved (e.g. by considering stream networks and actual water temperatures).

This freshwater ecology research group, in close cooperation with the hydrologists J.K., B.S. and N.F., works on the integration of hydrological and hydraulic models into SDMs and the analysis of how the incorporation of hydrological and habitat parameters may improve predictions.

Author contributions: S.C.J. and N.F. conceived the research; B.S. coordinated all Kielstau-related modelling campaigns; J.K. set up the hydrological and hydraulic model and the data transfer between models; and M.K. and S.D. set up the biological model. S.C.J. led the writing, and all authors contributed to the manuscript.

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