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A multi-scale, integrative modeling framework for setting conservation priorities at the catchment scale for the Freshwater Pearl Mussel *Margaritifera margaritifera*

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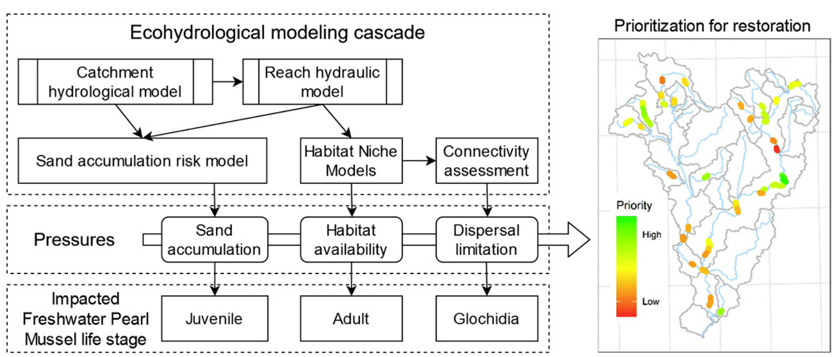
HIGHLIGHTS

- Ecohydrological modeling cascades support multi-scaled conservation planning.
- A tool for modeling the life stages of the Freshwater Pearl Mussels is developed.
- Hydrological, hydraulic, sand accumulation, species distribution models are linked.
- Sites for life-stage-specific conservation actions are identified and prioritized.
- Critical life stages drive choice of conservation action.

GRAPHICAL ABSTRACT



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ABSTRACT

The identification and prioritization of sites for conservation actions to protect biodiversity in lotic systems is crucial when economic resources or available areas are limited. Challenges include the incorporation of multi-scale interactions, and the application of species distribution models (SDMs) to rare organism with multiple life stages. To support the planning of conservation actions for the highly endangered Freshwater Pearl Mussel *Margaritifera margaritifera* (FPM), this paper aims at developing an ecohydrological modeling cascade including a hydrological model (SWAT) and a hydraulic model (HEC-RAS). Building on hydrology and hydraulics, Random Forest models for potential risk to juveniles due to sand accumulation, SDMs for adults habitat niche, and a landscape connectivity assessment of dispersal potential were developed. The feasibility of such models integration was tested in the Aist catchment (630 km^2) in Austria. The potential FPM habitat and the sand accumulation risk for the whole catchment were predicted with good accuracy. Results show that while the potentially suitable habitats for adults FPM cover 34% of the river network, only few habitat patches can maximize the dispersal potential (4% of the

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Conservation area prioritization

river network) and even less are showing limited impact of accumulations (3.5% of river network). No habitat patch that meets all the three criteria is available, suggesting approaches that target the patch-specific critical life stage-factors are promising for conservation.

1. Introduction

Freshwater ecosystems are facing declines in biodiversity exceeding those in terrestrial ecosystems, and are therefore considered one of the most threatened systems worldwide (Dudgeon et al., 2006; Geist, 2011). Habitat degradation, including physicochemical and morphological alteration, is among the drivers for biodiversity loss in lotic systems (Lopes-Lima et al., 2017; Ward et al., 2002). Effective conservation actions, including (i) identification of hotspots and reserve design, (ii) restoration ecology, and (iii) captive propagation and reintroduction are urgently needed to stop the declining trend of freshwater biodiversity (Strayer and Dudgeon, 2010). The identification and prioritization of sites where conservation efforts would be most effective is crucial when economic resources are limited (Engelhard et al., 2017; Hermoso et al., 2012). In this context, conservation planners face some major challenges in riverine systems.

First, planning of conservation actions at fine spatial scales is complicated by the highly dynamic, connected, directional, and hierarchical nature of rivers (Linke et al., 2011; Moilanen et al., 2008; Terrado et al., 2016; Ward et al., 2002). In riverine landscapes, interactions between processes acting at different spatial scales (e.g. catchment-scale hydrological patterns and reach-scale hydraulics) affect the success of local conservation actions, including ecosystem restoration (Barnas et al., 2015; Poff, 1997; Stoll et al., 2016). Recent developments successfully synthetized reach- and catchment-scale indicators for the prioritization of conservation actions (Kuemmerlen et al., 2019). However, they still rely on semi-empirical relationships, without considering the processes that support biodiversity at finer scales (Linke et al., 2019). Ecohydrological modeling cascades (EMCs) aim at integrating multiscale, process-based descriptions of the factors responsible for riverine biota distribution and diversity through sequences of loosely coupled models (Guse et al., 2015; Jähnig et al., 2012; Kail et al., 2015). EMCs have great potential for supporting the planning of conservation actions at the catchment scale.

Further challenges exist related to the application of species distribution models (SDMs) for prioritization approaches. SDMs are valuable tools when targeting restoration and reintroduction actions at broad spatial scales (Knight et al., 2011; Wilson et al., 2011). SDMs are used to deliver insights on the relationship between biota and the environment (Elith and Leathwick, 2009; Kuemmerlen et al., 2014; Vander Laan et al., 2013), and to prioritize conservation areas based on habitat quality (Gogol-Prokurat, 2011; Meller et al., 2014). However, the application of SDMs to rare and endangered organisms is challenging because data on species occurrence are often limited and clustered in space (Engler et al., 2004; Jarnevich et al., 2015). Moreover, few SDMs application exist for organisms with multiple life stages (Gallego et al., 2017; Taboada et al., 2013).

Finally, landscape connectivity is an important challenge in many modern conservation plans (Luque et al., 2012). Building on habitat quality, the assessment of connectivity (i.e. the extent at which organisms disperse between habitat patches) can provide a framework to prioritize sites for conservation actions (Erős et al., 2012; Saura and Pascual-Hortal, 2007). Several indices were developed for prioritizing the contribution of landscape patches to the overall landscape habitat connectivity (Saura and Rubio, 2010), but were rarely integrated for conservation planning in lotic systems (Buddendorf et al., 2019; Erős et al., 2012, 2018).

Freshwater mussels are important targets for conservation efforts because they are keystone elements of lotic fauna, providing relevant ecosystem services (Geist, 2010; Vaughn and Hakenkamp, 2001), and at the same time one of the most endangered group of animals on the planet (Lopes-Lima et al., 2017). Moreover, freshwater mussels are recognized as indicators of ecological integrity because of their high sensitivity for environmental perturbation (Farris and Van Hassel, 2006). The complex life cycle of the mussel includes a parasitic stage (glochidia) on a host fish, a juvenile stage buried in the hyporheic zone (i.e., the sediment or porous space beneath or adjacent to a streambed in which groundwater and surface water mix), and a benthic adult stage. All stages can be affected by environmental disturbances (Lopes-Lima et al., 2017; Quinlan et al., 2015). The Freshwater Pearl Mussel (FPM) *Margaritifera margaritifera* (L., 1758) is of particular interest because it exclusively inhabits cold running waters with low mineralization and low pH (Bauer, 1988). FPM populations have drastically decreased throughout Europe over the last century (Bauer, 1986; Hastie et al., 2000), lacking successful reproduction (Geist, 2010; Sousa et al., 2015). Therefore, FPM is now protected by the Bern convention (Annex III), the European Commission Habitat directive (Annex II and V), and is classified as "Critically Endangered" in Europe by the IUCN Red list of Threatened species (Cuttelod et al., 2011).

Sand and fine gravel accumulation (range of diameter: 1 mm–10 mm) is increasingly recognized as a key driver of FPM habitat degradation and population impairment due to its high mobility (Geist and Auerswald, 2007; Österling et al., 2010). The presence of adults have been related to refugia, i.e. sites where substrates are also stable during high flow events (Gangloff and Feminella, 2007; Howard and Cuffey, 2003; May and Pryor, 2016; Strayer, 1999). Sand and fine gravel are among the size classes that require the lowest critical velocity for the initiation of motion compared to coarser and finer size classes (Hjülström, 1935; Strayer, 2008). Habitats where sand and fine gravel accumulation is mobile during low flow are unfavorable for adult FPM that prefers substrates stabilized by gravel and boulders (Hauer, 2015). Moreover, excessive sedimentation of fines (<1 mm) can clog substrate interstices, limiting the oxygen diffusion between the water column and the hyporheic zone (Hastie et al., 2000), and lead to the accumulation of potentially toxic substances for juveniles (Scheder et al., 2015). Therefore, sites impacted by accumulation are of high priority for ecosystem restoration when the juvenile life stage is considered, while sites where the mobilization potential is low even during high flows are potentially good for adults.

Habitat fragmentation is also a major driver for active population impairment, limiting the FPM dispersal capacity (Schwalb et al., 2011). Dispersal between habitat patches can only occur during the obligate parasitic stage and is limited by the movement capacity of the host fish. FPM has high host fish specialization, limited to the Atlantic salmon *Salmo salar*, and the Brown trout *Salmo trutta* (Bauer, 1988). In Austria, the only host available is the Brown Trout, whose average movement distances are below 1 km (e.g. Höjesjö et al., 2015; Young et al., 2010). A good connectivity status is important for the recolonization of newly created habitats (Ferreira-Rodríguez et al., 2019; Schwalb et al., 2015) and to maximize the dispersal from supplemented populations.

Based on the knowledge gaps outlined above, the key question is which factors determine priority areas for conservation of FPM based on life-stage specific indicators. Thus, the aim of this study is to develop and test a novel, process-based, catchment-scale, evaluation approach to determine and prioritize potential FPM habitats for habitat restoration and conservation. The analysis builds on a habitat quality indicator for the adult life stage, a connectivity indicator for the parasitic stage, and a sand and fine gravel accumulation indicator for the juvenile life stage. The three layers are the basis of an integrative assessment for an improved management of FPM in the future. The models are implemented and linked for the Aist catchment (Austria).

2. Methods

2.1. The Aist catchment

The Aist catchment (630 km^2) is located in the eastern part of the state of Upper Austria (Fig. 1A, B), with an elevation ranging between 240 and 1100 m and a mean slope of 18% (DORIS, 2017). The bedrock is granite and gneiss (GBA, 2019), and sandy loam to silty loam Haplic Cambisols (Hengl et al., 2017) are the prevalent soil type. The land use

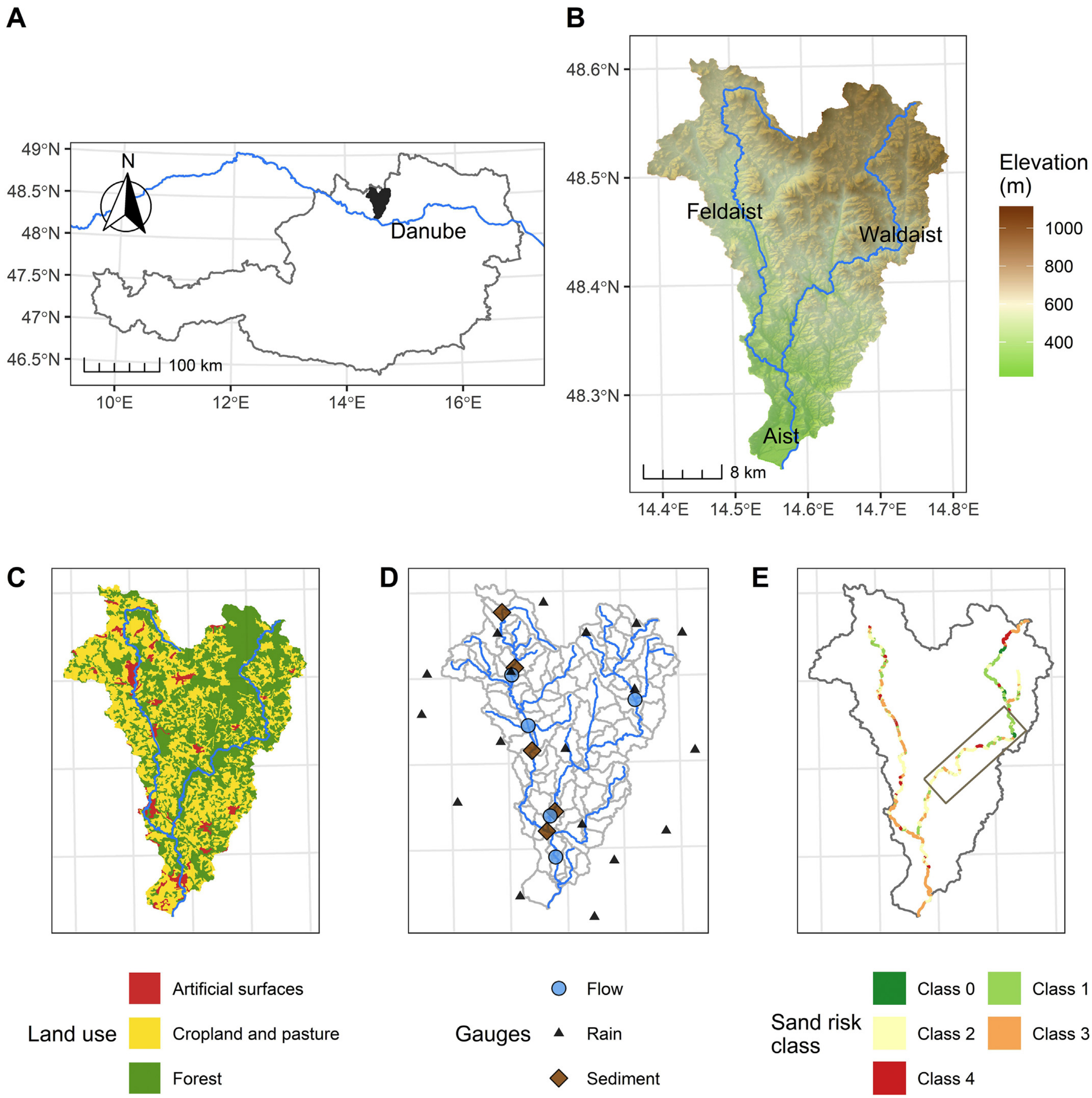

Fig. 1. A) position of the Aist catchment in Austria; B) Terrain elevation and position of the main channels in the Aist catchment; C) Land use; D) Models extents: polygons represent SWAT models subcatchments, polylines represent HEC-RAS modeled reaches; points represent rain, flow and sediment gauges used in SWAT; E) Mapped sand accumulation risk in the main channels: class 0 = No alteration of the natural substrate; class 1 = Little disturbance due to sand accumulation; class 2 = Some habitat changes but main morphological features are kept; class 3 = Mesohabitat is fully covered by sand accumulations; class 4 = Mesohabitat is fully covered by sand accumulations, that are mobile during low flow conditions. The grey rectangle shows the river reach where Freshwater Pearl Mussel data are available.

is dominated by forests (47%) and agriculture (49%), with limited area occupied by settlements (4%; Büttner, 2014). The climate is temperate, with an average yearly temperature of 7.1 °C and an average yearly precipitation of 835 mm (HDLO, 2017). The Aist River flows north to south and forms after the confluence of two main tributaries, the Feldaist and the Waldaist (Fig. 1C). The Feldaist drains an agriculture/pasture dominated landscape and the Waldaist drains a pasture/forest dominated landscape. The average multiannual flow at the confluence of the Aist with the Danube is 6.4 $m^3 s^{-1}$ (HDLO, 2017). Rivers in the Aist catchment are classified as "plane bed" with cobbles and sands as dominating substrates (Leitner et al., 2015; Montgomery and Buffington, 1997), while steep sections are classified as "cascade type" with a boulder substrate (Hauer, 2015). The Aist catchment hosted a FPM population with >20,000 specimens occupying 30 km of river length in the early 1990s (Ofenböck et al., 2001). Less than 3000 individuals are left in the eastern tributary, the Waldaist. Nevertheless, the remnant population is still relevant for regional genetic diversity (Geist, 2010). The Waldaist River is part of the Natura 2000 site "Waldaist and Naarn" (AT3120000).

2.2. Ecohydrological modeling cascade

The proposed EMC (Fig. 2) is composed of a sequence of models structured in a way that the outputs from the coarser spatial scale can be used as inputs to finer scale models (Kiesel et al., 2013):

(i) the ecohydrological Soil and Water Assessment Tool 2012 (SWAT, Arnold et al., 2012a, 2012b) for discharge and sediment generation and transport at the catchment scale;
(ii) the hydrodynamic numerical 1D-model hydraulic Engineering Centre – River Analysis System (HEC-RAS, Brunner, 2002) for reach scale hydraulics;
(iii) a Random Forest (RF, R package 'caret'; Kuhn, 2008; R Core Team, 2019) for sand and fine gravel accumulation at the reach scale;
(iv) Species Distribution Models (SDMs, R package 'biomod2', Thuiller et al., 2009) for the FPM distribution at the reach scale;
(v) a connectivity assessment at the catchment scale based on SDMs habitat quality results (CONEFOR, Saura and Torné, 2009).

Hydrological outputs from SWAT were used as inputs to HEC-RAS. Predictors were generated from SWAT and HEC-RAS outputs and from the land use map and used as inputs for RF, SDMs, and CONEFOR. The sand accumulation modeled with the RF was the basis to evaluate priority sites for juveniles. The suitable habitats identified by SDMs and the relative distances were used as inputs for CONEFOR. CONEFOR outputs include habitat quality indicators for adults and a connectivity assessment for dispersal potential between suitable habitat patches (defined in Section 2.8). The models are described in Sections 2.3–2.8.

2.3. Hydrological modeling

SWAT is a semi-distributed, process-based hydrological model (Arnold et al., 2012a, 2012b) with the capability to simulate water and sediment fluxes for a watershed with daily time step. In SWAT, river basins are partitioned into sub-catchments (Fig. 1D), and are further

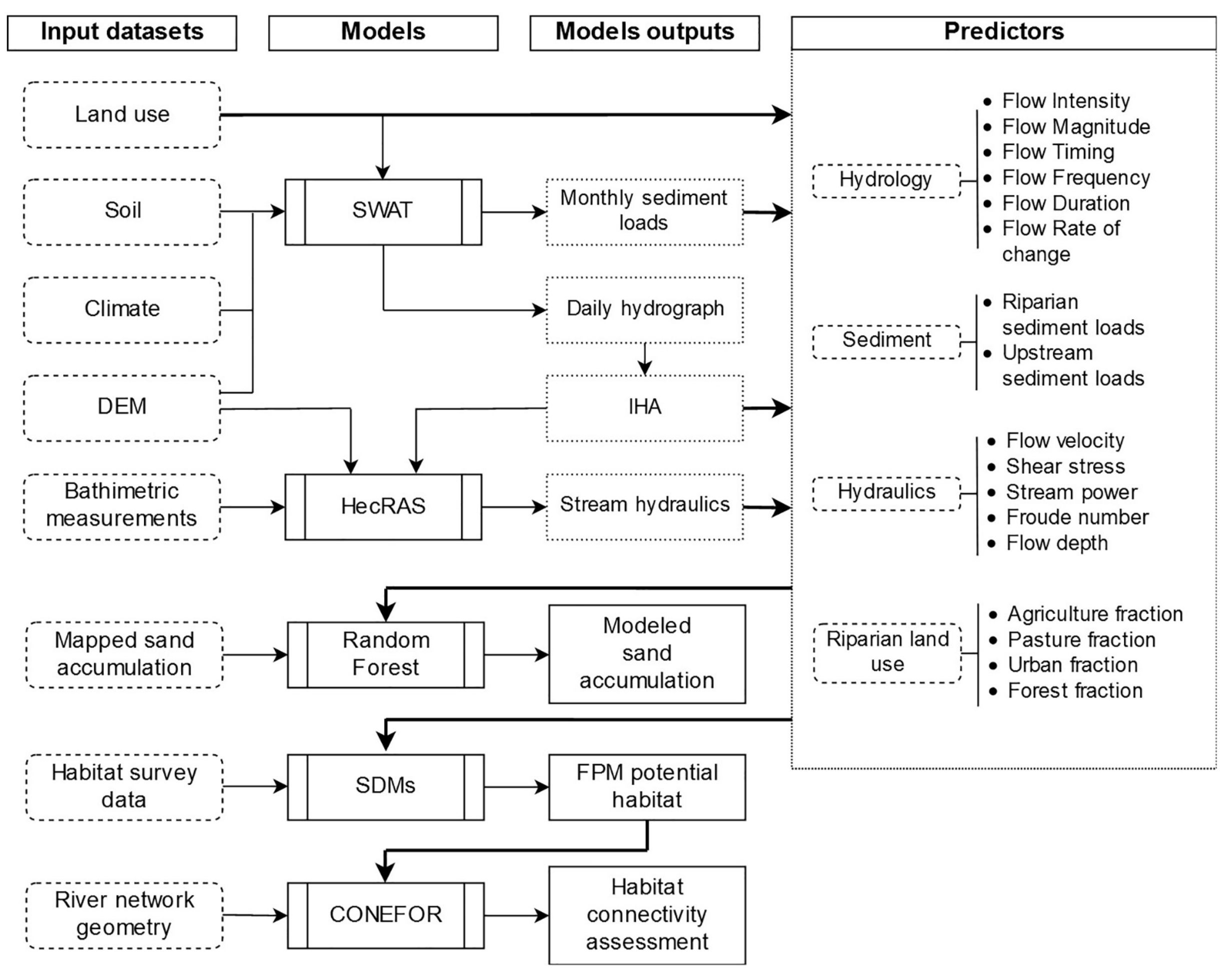

Fig. 2. Ecohydrological modeling cascade. Arrows represent flows of information. IHA = Indicators of hydrological alteration; SDMs = Species Distribution Models. Refer to the text for the meanings of the models acronyms.

subdivided into uniformly responding landscape units (hydrological response units, HRUs). Water and sediment balances are computed at the HRUs level, aggregated to sub-catchments, and routed to the catchment outlet through the river network (Arnold et al., 2013). SWAT provides simulated fluxes at the sub-catchment outlets with daily and monthly time step as output.

A digital elevation model (10 × 10 m; DORIS, 2017), a soil map (250 × 250 m; Hengl et al., 2017) combined with the pedotransfer functions approach from Saxton and Rawls (2006), a generic land use map (Corine Land Cover 2012, minimum mapping unit 25 ha), an agricultural land use map (10 × 10 m BMLFUW, 2019), climatic data from 15 weather stations (HDLO, 2017), and point sources information (LODUWAW, 2017) were used in ArcSWAT 2012.10.4.19, an ArcGIS graphical user interface to setup the model (Table S1 in the supplementary material). The catchment delineation process resulted in a subdivision of the catchment in 103 sub-catchments (Fig. 1D, area: 6.0 ± 3.1 km^2, reach length: 5.5 ± 2 km, mean ± SD) and 267 HRUs. The model v2012 rev. 664 was used for simulations.

The SUFI2 algorithm (Abbaspour et al., 2004) within the software SWAT-CUP v5.1.6.2 was used for model calibration, validation, sensitivity, and uncertainty analysis following the protocol described by Abbaspour et al. (2015), using the objective function Kling-Gupta efficiency (KGE, Gupta et al., 2009). This optimization process is referred to as 'hard' calibration in opposition to 'soft' calibration with qualitative data (Seibert and McDonnell, 2002; Yen et al., 2016). The calibration followed a two-step approach. First, average daily streamflow data from five gauging stations (HDLO, 2017; Figs. 1D, S1) were used for calibration of the daily water flows. Second, monthly water flows and sediment fluxes were calibrated. Before the second calibration, upland sediment production was 'soft' calibrated to match the values reported by similar studies in the Danube catchment (Vigiak et al., 2017). Due to low frequency of grab sample data (LODUWAW, 2017), the USGS load estimator software (LOADEST, Runkel et al., 2004) was used to develop regression models for five sampling locations (Fig. 1D; Table S2) for the 'hard' calibration of monthly-averaged sediment loads (t $month^{-1}$) and water flows using SUFI-2. Since some parameters were sensitive for both sediment and flows, water flows were used also in this second step to allow for compromise optimization. Finally, the model performance for streamflow was evaluated again at a daily time step to control a possible deterioration in the fitting capacity. The model was calibrated for the period 2006–2010 and validated for 2011–2016.

The 20th, 50th, and 90th flow percentiles, corresponding to low flow, medium flow, and high flow conditions, were extracted from the daily hydrographs at the sub-catchment outlets and used as input to perform static flow profiles in HEC-RAS. Points in the reaches where flow is changing (i.e. where the HEC-RAS modeled reach crosses a SWAT sub-catchment outlet or where the discharge increases) were imported in HEC-RAS as point flow changes.

2.4. Hydraulic modeling

Hydraulics calculations were carried out for the Feldaist and his tributaries ($n = 10$ reaches, length between 3.4 km and 32.6 km), the Waldaist and his tributaries ($n = 7$; reach length between 4.5 km and 61.0 km) and for the Aist and his tributaries ($n = 3$; reach length between 7.3 km and 21.8 km) for a total of 20 reaches (Fig. 1D). Implemented hydrodynamic-numerical 1D-models were based on a digital elevation model (Airborne Laserscan, 1 m × 1 m, data source: Government of Upper Austria). Additionally, a bathymetric surveying of the Feldaist and the Aist was carried out by total stations (e.g. Leica TC805) with minimum 10 points per cross section. The digital elevation model for the lower reach of the Feldaist and the Aist was provided by the Government of Upper Austria and based on the study of Hauer (2015). Hydraulic calculations on the Waldaist and its tributaries could only be performed on the basis of the digital elevation model neglecting the bathymetry below the airborne scanned water surface elevation. The model setup was performed with the ArcGIS interface HEC-GeoRAS v10.2 with an average cross sectional distance of 25 m. Hydraulics were calculated in HEC-RAS v5.0.5 for a total amount of 11,032 cross sections. The calibration was performed in selected sites in the Feldaist and Aist by measuring in the field the discharge and the water elevation during low flow conditions and comparing it to the results of the models for a total reach length of 38.77 km. In those sections where only Airborne Laserscan data was available, a sensitivity analysis (altering the bed roughness) was performed.

2.5. Hydrologic, sediment, hydraulics, and land use predictors

Three different classes of predictors were generated based on SWAT and HEC-RAS outputs: (i) SWAT-based hydrological predictors, (ii) SWAT-based sediment predictors, and (iii) HEC-RAS-based hydraulics predictors (Fig. 2). In addition, land use predictors were extracted from the land use map.

Indicators of hydrological alteration (IHAs, package 'EflowStats') were used to generate ecologically relevant predictors from the SWAT daily hydrograph. IHAs describe duration, frequency, timing, magnitude, and rate of change of flow events (Olden and Poff, 2003). One metric for each category within the complete set of 171 IHAs was selected to minimize the predictor's redundancy with a pairwise collinearity analysis and a principal component analysis. When the pairwise correlation exceeded the 0.7 threshold, the metric with lower loading on the most significant axis was removed from the list (Kakouei et al., 2017). Magnitude IHAs were excluded from the analysis, because they are implicitly accounted for in the flow percentiles used as inputs to the hydraulic model.

Sediment load percentiles were computed from the local sub-catchment SWAT output and normalized for channel length using:

$$S_{i,p} = S_{SWAT,i,p} \frac{A_i}{L_i} \tag{1}$$

where, for sub-catchment i and load percentile p: $S_{i,\ p}$ is the sediment load to the channel (t km^{-1}), $S_{SWAT,\ i,\ p}$ is the SWAT sediment (t ha^{-1}), A_i is the area of the sub catchment (ha), L_i is the length of the channel (km). S_i was computed for 50th and 90th sediment load percentiles to account for mean and high flow conditions. A cumulative variant of sediment load indicators was also computed using the cumulative upstream sediment yield.

HEC-RAS cross-section outputs contained several hydraulic parameters, including flow velocity (m s^{-1}), flow depth (m), Froude number (−), and shear stress (Pa) and were used as predictors. Additionally, the specific stream power (W m^{-1}) was calculated out of HEC-RAS outputs. Finally, the riparian land use for each HEC-RAS cross section was calculated as fractions of agricultural, pasture, forested, and urban land uses using a 100 m circular buffer.

All the predictors were resampled at a 50 m resolution to produce the environmental raster layers for RF and SDMs (see Table 2 for the predictors selected for the consecutive modeling steps; Table S7 for the complete list). A time window starting 10 years before the collection of the data fitted with RF and SDMs was selected to calculate averaged predictor values. Hydrological and sediment predictors from SWAT were calculated at the sub-catchment level without any spatial interpolation, assuming a limited spatial variability within the single sub-catchments because of the reduced number of HRUs per each sub-catchment.

2.6. Sand and fine gravel accumulation modeling

The extensive substrate composition mapping described in Hauer (2015) was used to train the RF. The degree of alterations in river morphology due to deposited material was mapped during an extensive field work campaign between December 2013 and July 2014 according to the hydro morphological status of a water body under the Water Framework Directive (LAWA, 2000; BMLFUW, 2010). The local habitat degradation was classified into five risk classes ranging from no disturbance (class 0) to significant habitat degradation (class 3) to highly mobile sediments during low flow conditions (class 4; for details see Table 1; Figs. S7, S8; Hauer, 2015). Class 3 is potentially harmful for juveniles because of the potential development of clogged interstices, class 4 is potentially harmful also for adults because of the lack of substrate stability.

Random Forest models (Breiman, 2001) were used to fit the mapped substrate with hydrological, sediment, and hydraulics predictors (Table 2). The input dataset was randomly split in a calibration set (70%) and validation set (30%). The calibration dataset was used with a 10-fold cross validation to tune the model's hyperparameters (Strobl et al., 2009) and fit the RF. Features were selected using the approach described by Haddadchi et al. (2018). A short list of 8 predictors were selected from the available predictors based on expert opinion and used for fitting, while the 'VSURF' package (Genuer et al., 2015) was used to detect redundant predictors. Predictor importance was assessed as the mean decrease in accuracy when the predictor is randomly permuted (Breiman, 2001). The model goodness was evaluated using the accuracy (i.e. the fraction of sites correctly classified) and the Kappa statistics (i.e. the accuracy normalized by the accuracy that may result from random sampling) from the independent dataset confusion matrix (Allouche et al., 2006).

Finally, an index was defined to synthetically describe the accumulation risk status of a single habitat patch. Following the indications in Kuemmerlen et al. (2019), the accumulation risk index (ARI) of each habitat patch was defined as the average between the worst and the average risk scores of raster cells belonging to the patch. Therefore, ARI assumes continuous values between 0 (no alteration) and 4 (severe alteration).

2.7. Species distribution models

An available dataset resulting from an extensive mapping of the Waldaist was used to fit the SDMs. The data were collected in October 2010 for a 400 m river reach (Jung et al., 2013), and in May 2016 for a 25 km reach (Huemer et al., 2016). FPM sub-populations occur in 69 points. Presence-only data from the dataset were used to fit the model to disentangle realized and potential habitat distributions (Marcer et al., 2013). The input dataset was split into a training set (70%) and a testing set (30%).

The "biomod" modeling procedure employs several algorithms and provides an ensemble forecasting to reduce uncertainties related with the choice of the modeling algorithm (consensus model, Thuiller et al., 2010) and to improve the robustness of the forecast (Araújo and New, 2007). Different modeling techniques were used, including a generalized linear model (GLM), a generalized additive model (GAM), a generalized boosting model (GBM), and a maximum entropy model (MaxEnt). Each algorithm used a high number of pseudo absences (500), and a 10-fold cross validation following the indications by Barbet-Massin et al. (2012), for a total of 40 fitted models. Because of the small size and spatial coverage of the dataset used to train the SDMs, only hydraulic and riparian land use predictors were used to fit the models (Jähnig et al., 2012).

Table 1
Sand and fine gravel accumulation risk classes. The classification holds for different morphological features (plane bed, riffle, pool; Hauer, 2015).

Risk class	Description
0	No alteration of the natural substrate
1	Little disturbance due to sand accumulation
2	Some habitat changes but main morphological features are kept
3	Mesohabitat is fully covered by sand accumulations
4	Mesohabitat is fully covered by sand accumulations, that are mobile during low flow conditions

The ensemble model results from the weighted average of the single algorithm models (Marmion et al., 2009) by multiplying the Area Under the Receiving Operating Characteristic Curve (AUC) scores with a decay of 1.6 (Jähnig et al., 2012). Metrics used for assessing model performances (Allouche et al., 2006) were the Area Under the Receiving Operating Characteristic Curve and the True Skill Statistics (TSS, the sum of sensitivity and specificity). The output of the ensemble model is the spatial distribution of the Habitat Suitability Index (HSI, range 0 to 1). A threshold that balances omission and commission errors was applied to the Habitat Suitabiliy Index to discriminate suitable and unsuitable habitats (Bean et al., 2012).

2.8. Connectivity assessment

To estimate connectivity, landscapes can be conceptualized as a graph where the nodes are habitat patches and the links are paths between nodes (Erős and Campbell Grant, 2015). Habitat patches and links are associated with qualitative attributes describing the habitat quality and the goodness of the connection provided by the links (Saura and Pascual-Hortal, 2007). Following this approach, the overall landscape connectivity can be defined as the sum of the probabilities that two habitat patches randomly placed in the landscape are reachable from each other, given a set of n patches and p_{ij} connections among them (Table 3). For this purpose, the software CONEFOR v2.6 (Saura and Torné, 2009) was used to compute the probability of connectivity index (PC, Saura and Pascual-Hortal, 2007).

The use of the PC index implies the following assumptions: (i) FPM uses exclusively the identified habitat patches, without colonizing additional sites; (ii) the distance between patches is a proxy for movement cost of the host fish; (iii) parasitized host fish (Brown trout) dispersal is symmetrical (iv) the contribution to dispersal of glochidia not attached to the host fish gills is negligible.

Habitat patches used in the definition of the graph were defined as aggregates of contiguous suitable raster cells within a river section longer than 300 m. The defined patches were then used as planning units for conservation actions. The relative importance of each habitat patch (dPC) was calculated as the relative connectivity drop when the patch is removed from the landscape graph (Saura and Rubio, 2010). The habitat quality attribute used in the index calculation was the sum of the habitat suitability indices of all the cells within one patch, i.e. the Weighted Usable Area of the habitat patch. The link quality was modeled with a negative exponential probability density function accounting for inter-patch dispersal in relation to fish movement (Table 3), using river-network interpatch distance (package 'riverdist'). Following the indications in Höjesjö et al. (2015) and Young et al. (2010), the probability of observing Brown trout movement distances >1 km was set to 0.5. The consistency of the prioritization was assessed by testing different dispersal distances (250 m to 2 km) and comparing the rankings using the Spearman's coefficient (Engelhard et al., 2017).

The dPC index can be decomposed in complementary and comparable fractions describing the different roles of habitat patches (Saura and Rubio, 2010; Table 3). The dPCintra fraction represents the habitat quality of a habitat patch and rescales the habitat quality attribute used to calculate PC. The dPCflux fraction describes the potential of a patch to generate or receive dispersal fluxes and depends on both the habitat quality attribute and the relative position of patches on the graph. The dPCconnector fraction represent the patch role as a stepping stone for movement through the network and neglects the habitat quality attribute.

Table 2
Environmental predictors used for the fine sediment accumulation model (RF) and for the species distribution model (SDMs).

Name	Long name	Description	Units	Source	Used in
LTs_up_90	Upstream peak sediment load	90th percentile of the SWAT sediment yield normalized by the drainage density and cumulated for upstream subcatchments	$t\ km^{-1}\ month^{-1}$	SWAT	RF
dh3	Annual maxima of 7-day means of daily discharge	Magnitude of maximum annual flow for weekly duration	$m^3\ d^{-1}$	SWAT	RF
dl15	Low exceedance flow	Mean magnitude of multiannual flows exceeded 90% of the time divided by median daily flow	–	SWAT	RF
fl2	Variability in low flow pulse count	Coefficient of variation of number of annual occurrences during which the magnitude of flow is below the 25th percentile of daily	–	SWAT	RF
fh5	Flood frequency	Mean yearly number of events where the flow exceeds two times the median discharge	–	SWAT	RF
v_LF	Flow velocity during low flow	Cross sectional average of flow velocity calculated with the 10th discharge percentile	$m\ s^{-1}$	HEC-RAS	SDMs
v_MF	Flow velocity during mean flow	Cross sectional average of flow velocity; calculated with median discharge	$m\ s^{-1}$	HEC-RAS	RF
SS_HF	Shear stresses during high flow	Cross sectional average of shear stresses, calculated with the 90th discharge percentile	Pa	HEC-RAS	RF, SDMs
d_MF	Flow depth during mean flow	Cross sectional average of flow depth; for median discharge	m	HEC-RAS	RF
SPs_LF	Specific stream power for low flow	Cross sectional average of specific stream power calculated with the 10th discharge percentile	$W\ m^{-1}$	HEC-RAS	RF
LU_FR_rip	Riparian forest	Fraction of forest land use in a 100 m radius buffer	–	Land use map	SDMs

3. Results

3.1. Models performance

The calibrated SWAT performed well with monthly stream flow and sediment loads (Figs. S2–S4), with a Kling-Gupta Efficiency (KGE, mean ± standard deviation represent variability between flow or sediment gauges) of 0.70 ± 0.12 for flow and 0.67 ± 0.21 for sediment in the calibration period, and 0.78 ± 0.10 for flow and 0.63 ± 0.17 for sediment in the validation period (Tables S4, S6, S7 for the models performance and S3, S5 and S6 for the calibrated parameters). This is acceptable according to the widely used model evaluation guidelines by Moriasi et al. (2015). The deterioration of the objective function value when using monthly-calibrated parameters for daily flow simulations was limited (KGE = 0.73 ± 0.02 in the calibration period and KGE = 0.70 ± 0.08 for validation; mean ± standard deviation) and allowed for monthly simulations for sediment loads and daily simulations for flow (Table S7). The difference between the measured and the calculated (using HEC-RAS) water surface was always <3 cm, and considered acceptable (Bolla Pittaluga et al., 2014; Miori et al., 2006; Owens et al., 2005).

The sand accumulation model showed a good discriminatory capacity (test dataset performance metrics: Accuracy = 0.70, Kappa = 0.60; compare with Belgiu and Drăgu, 2016; Diesing et al., 2014; Lawrence et al., 2006). The uncertainty related to predictor values outside the training ranges was low and constrained only to few small tributaries (Fig. S11). The important controlling factor were local hydraulics (flow depth and shear stresses) and upstream sediment loads (Figs. S8, S9). Classes 3 and 4 were more likely when shear stress is low and flow depth is high, while low risk classes were more likely when shear stress is high. Classes 0–3 also showed a dependence on the upstream sediment loads, while class 4 did not. Most of the catchment area (37%) is at moderate risk (class 2), whereas high-risk classes 3 and 4 occupied 14% and 4% of the reach cells, respectively (Fig. S12). ARI ranged between 0 and 4, with a mean value of 1.9 (Fig. 4B), with only few habitat patches being free from accumulations (ARI < 1 for 3.5% of the river network).

The ensemble habitat model has good discriminatory capacity (Area Under the Receiving Operating Characteristic Curve = 0.88, True Skill Statistics = 0.61, Sensitivity = 0.87, Specificity = 0.73, compare with Domisch et al., 2013). The predictors used in the final models were (i) high flow shear stresses, (ii) riparian forest cover, and (iii) flow velocity during low flows. High flow shear stress was identified as the most influential predictor of the three. The partial dependence plots of the ensemble model (Fig. 3) describe the FPM habitat response to the predictors' gradients. The most suitable habitats are predicted to occur for shear stress of 15 Pa, corresponding to different substrate stabilities when expressed in terms of Shields parameter (Shields, 1936). The Shield parameter for 15 Pa is >0.08 for sand and fine gravel accumulations, and is smaller than 0.01 for grain sizes >5 cm, the first being fully mobile and the latter being stable (May and Pryor, 2016, Fig. S13). Decreasing suitability is observed for higher shear stresses (Fig. 3A). High riparian forest cover affects positively the habitat for values above 70% (Fig. 3B). The dependency from low flow velocity has an optimum value for 0.27 $m\ s^{-1}$, and lower suitability for sites with either very low or very high flow velocities (Fig. 3C). The ensemble model predicts 34% of the stream network area to be potentially suitable for adult FPM. The optimal values identified by the model are representative of in-field conditions. In fact, no significant differences in predictors' values were detected between the sites where FPM is predicted to

Table 3
Definitions and equations of the probability of Connectivity (PC) index and his components dPCintra, dPCflux, and dPCconnector (Saura and Rubio, 2010).

Index	Description	Formulation	Details
PC	Probability of connectivity	$PC = \sum_{i=1}^{n}\sum_{j=1}^{n} a_i \times a_j \times P_{ij}^{*}/A^2$	a_i and a_j are the habitat quality values of the two habitat patches; A is the total suitable area of the landscape; p_{ij}^{*} is the probability of colonization
Dispersal probability		$P_{ij}^{*} = \exp\left(-\alpha d_{ij}\right)$	α is the inverse of the species dispersal distance; d_{ij} is the effective distance between patches i and j
dPC	Relative importance of cell k for landscape connectivity	$dPC_k = \frac{(PC - PC_{remove,k})}{PC} \times 100$	$PC_{remove,\ k}$ is the PC index of the landscape when the patch k is removed
dPCintra	habitat suitability of a specific habitat patch	$a_i \times a_j$ $when\ i = j = k(a_k^2)$	Depends only on the habitat patches attributes and not on the distances
dPCflux	area-weighted dispersal flux based on the position and attributes of the patches mosaic	$a_i \times a_j \times P_{ij}^{*}$ $when\ i = k\ or\ j = k\ and\ i \neq j$	Depends on the number of incoming/outgoing connections and the attributes of the nodes.
dPCconnector	Importance of a patch as stepping-stone	$a_i \times a_j \times P_{ij}^{*}$ $when\ i \neq k, j \neq k$	Depends on the topology of a node and his irreplaceability as a link between nodes.

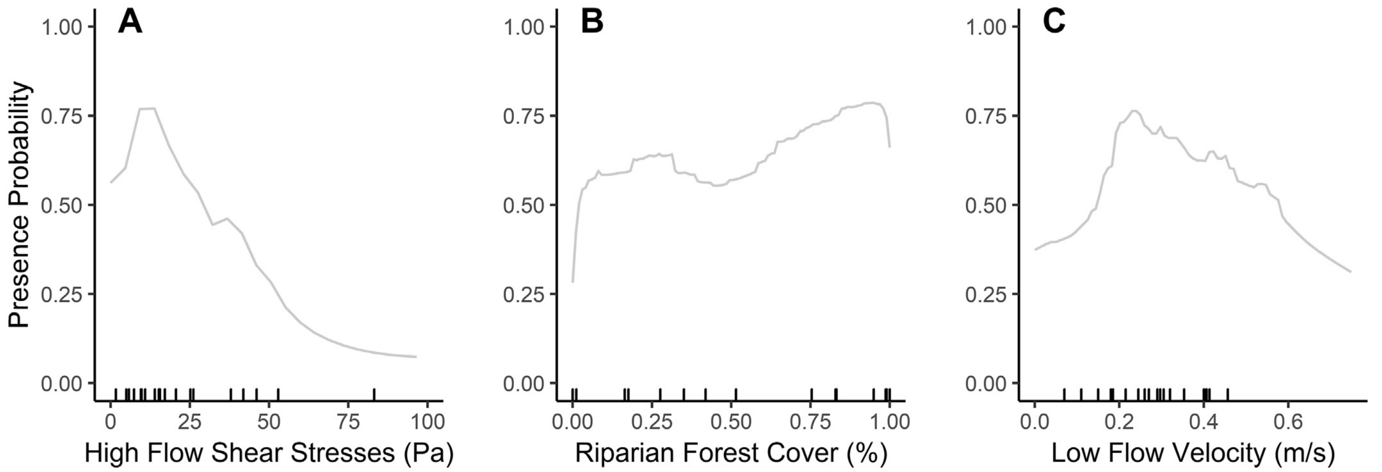

Fig. 3. Partial dependence plots showing the dependence of probability of presence of FPM from a predictor gradient when the other predictors are constant on their modal values. A) dependence from shear stresses during high flow; B) dependence from riparian forest cover; C) dependence from flow velocity during low flow. Ticks on the horizontal axis represent the predictors' values densities.

occur and sites where it has been sampled (Table 4, Mann-Withney *U* test, $p > 0.37$ for all predictors), meaning the existing FPM habitat is effectively represented by the model (Jähnig et al., 2012).

3.2. Connectivity assessment

A total of 39 habitat patches that are potentially suitable for conservation actions were identified (mean patch length: 750 m, maximum patch length: 1800 m, Fig. 4), covering 10% of the river network. The coverage is lower than the potential extent predicted by the habitat model because small patches were excluded. The patch contribution to the overall landscape WUA was variable (minimum: 1.5%, maximum: 6.4%, mean: 2.5%; Fig. 4A).The dPC index showed a high variation range (mean: 3, minimum: 0.99, maximum: 11). The two fractions that contribute more to the dPC index were dPCintra (mean: 1.8, minimum: 0.5, maximum: 9.8; Fig. 4C) and dPCflux (mean: 1.5, minimum: 0.01, maximum: 9.8; Fig. 4D). The dPCconnector did not significantly contribute to the overall connectivity (mean: 1.6 10^{-8}, minimum: 0, maximum: 3.1 10^{-7}). The 10 most relevant habitat patches (Fig. 6) account for 56% of the landscape dPCintra and 61% of dPCflux. Important patches for dPCflux correspond to 4% of the total reach area (Table S9).

The choice of the dispersal distance did not significantly affect the habitat patch ranking for all the tested perturbations of the selected 1 km dispersal threshold. The minimum Spearman's coefficient was always above 0.95 for both dPC and dPCflux. A sensitive drop (<0.9) was observed only when the dispersal distance is lower than 250 m. The dPCintra was not sensitive to dispersal distance because it was computed solely on the base of patch quality attributes.

The correlation between the dPC components and the patch WUA was explored with linear models: as measured by R^2, the weighted usable area explains 95% of the variance of dPCintra ($p < 0.001$), 49% of the variance of dPCflux ($p < 0.001$), and shows a non-significant relationship with dPCconnector ($p > 0.05$). Finally, no correlation between ARI and all the connectivity fractions was detected with a linear model ($p > 0.05$ for all fractions).

4. Discussion

4.1. Modeling framework

Successful conservation actions require not only the knowledge of species-specific habitat niches (Wilson et al., 2011), but also studies able to assess potential impacts of pressures (Santos et al., 2015). While FPM habitat niche studies are common (Geist and Auerswald, 2007; Quinlan et al., 2015), fewer studies on pressures and relative impacts are available (Bolotov et al., 2018; Österling and Högberg, 2014; Santos et al., 2015). The existing studies rely on empirical linkages that do not explain the mechanistic processes linking pressures and impacts on different life stages of FPM populations (Beechie et al., 2010), thus lacking the generalization and projection power needed to support targeted conservation actions at the catchment scale.

This study is a step forward in the development of process-based tools capable to (i) identify the sites with high habitat quality using in stream predictors from a multi-scale approach (Gumpinger et al., 2014), (ii) prioritize sites for conservation actions in a riverine landscape ecology perspective (Newton et al., 2008), (iii) complement the habitat and connectivity information with additional pressures layers, and (iv) combine the different layers for an integrative prioritization, in this case for multiple life stages. In fact, the structure of the proposed modeling framework is flexible and multiple pressures (e.g. nutrients, dissolved organic matter) or indicators could be implemented as additional layers for a final prioritization.

4.2. Adult Freshwater Pearl Mussel habitat niche

FPM is predicted to occur within a narrow habitat niche (Table 4, Fig. 3), consistently with the findings in Wilson et al. (2011), requiring low shear stress during high flow events, high extent of riparian forest cover, and medium flow velocities during low flows. Shear stress is widely recognized as an important factor limiting freshwater mussel richness and abundance and controlling dislodgement risk (Allen and

Table 4
Mean values of the modeled variables at the FPM sampling sites, at the sites where FPM is predicted to occur, and variables ranges in the Aist catchment. Mann-Withney U test between sampling sites and predicted occurrence sites was not significant ($p > 0.37$ for all predictors).

	Sampling sites (±SD)	Predicted occurrence (±SD)	Aist catchment
Shear stresses (Pa) during high flow	15.9 (±10.9)	15.9 (±8.2)	0–455
Flow velocity ($m\ s^{-1}$) during low flow	0.27 (±0.10)	0.27 (±0.08)	0–3.20
Forested riparian land use (%)	0.67 (±0.33)	0.70 (±0.30)	0–1

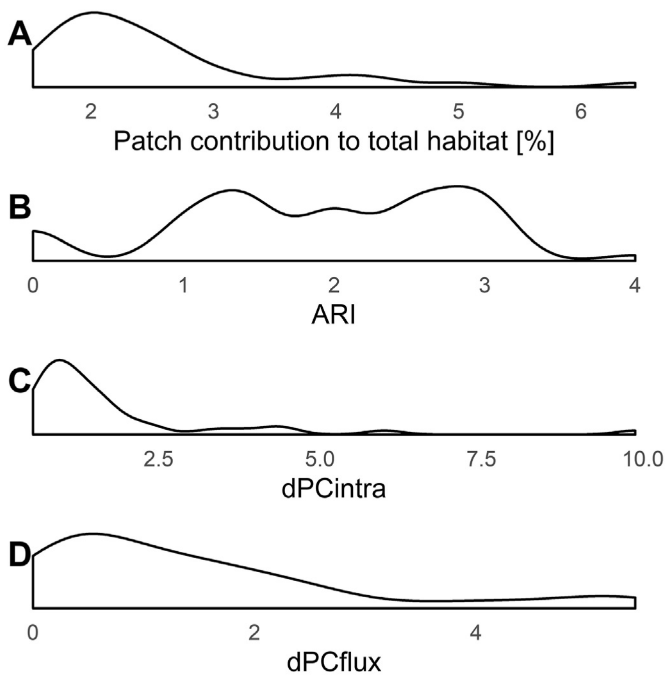

Fig. 4. Density plots of: A) Patch contribution to total habitat; B) Accumulation Risk Index (ARI); C) dPCintra; D) dPCflux.

Vaughn, 2010; Quinlan et al., 2015; Scheder et al., 2015). The modeled response to shear stress is valid for the 10th discharge percentile, comparable with the bankfull discharge, when the maximum transport capacity of the river section is activated (Doyle et al., 2007). These findings are coherent with the 'refugia' hypothesis (Strayer, 1999): the analysis of the Shields parameter shows that the sand and fine gravel accumulations are unstable when Shear stresses are optimal for adults FPM, while coarser substrates are stable. (May and Pryor, 2016). The presence of riparian forests is an indication that a section of river was not disturbed or modified recently by bank re-sectioning or channel dredging (Hupp, 1992; Österling and Högberg, 2014). The optimum dependency on flow velocity values was also reported by Hastie et al. (2000). Quinlan et al. (2015) identified low flow velocities as a controlling factor for oxygen diffusion into the hyporheic zone and as a limiting factor for the efficiency of water filtration.

Among existing conservation strategies, captive breeding (Buddensiek, 1995; Ofenböck et al., 2001), habitat and catchment restoration (Hauer, 2015; Horton et al., 2015), or a combination of the two (Kyle et al., 2017) are increasingly considered as feasible options to reverse the decline of existing populations or to reintroduce the FPM where it historically existed (Wilson et al., 2011). The knowledge of the adult FPM habitat niche is therefore essential for both the identification of sites for reintroduction and the identification of parameters to guide the design of habitat restoration.

4.3. Sediment accumulation and potential impact on the juvenile life stage

In the Aist catchment, relevant sources of sediment are soil erosion due to agricultural land use (as found in other catchments by Altmüller and Dettmer, 2006; Knott et al., 2019; Popov, 2015; Pulley et al., 2019) and increased bedrock weathering due to acidification of soils by spruce tree forestry (Hauer, 2015). Sediment production is estimated with the Modified Universal Soil Loss Equation (MUSLE, Neitsch et al., 2011), which describes the complex processes involved in sediment generation and transport with a lumped formulation that does not involve bedrock weathering. Despite this simple limitation, the spatial variability of sediment production is implicitly captured by HRUs-based landscape discretization in SWAT, allowing for the inclusions of sediment connectivity in the sand accumulation assessment (Fryirs et al., 2007). In addition, the influence of bank erosion and anthropogenic alterations of river geometry as a negative impact on habitat quality has to be discussed for possible relevance of habitat degradation (Flödl and Hauer, 2019; Pulley et al., 2019). This could be included by adding additional modules to the framework to account for channel-forming geomorphological processes and bank erosion (Kail et al., 2015).

A clog-free sediment matrix is a necessity for juveniles and young mussels that stay in the substrate for up to 10 years (Bauer, 1988; Buddensiek, 1995). In some parts of the river (4%), sand fractions become mobile even at low flow conditions, which severely degrades the habitat for adult FPM. The extent that is degraded for juveniles (classes 3 and 4) is much higher (18%). In general, juveniles have been identified as the most sensitive life stage of FPM (Österling et al., 2010), and therefore an assessment of potential suitability for juveniles, like it was done in the presented study, is needed for an effective conservation plan.

4.4. Potential dispersal of glochidia

Our connectivity assessment revealed that the potential dispersal between habitat patches is explained not only by the habitat quality, but also by the relative positions within the river network. Also, the low value of dPCconnector suggests dispersal occurs between contiguous habitat patches. The lack of connectivity between suitable mussel habitats has been highlighted as the cause of the imbalances between local colonization and extinction rates (Allen and Vaughn, 2010). This is primarily related to host fish mobility (Schwalb et al., 2011), with little contribution from glochidia drift due to their limited survival rate in the water column (Akiyama and Iwakuma, 2007). Similar results on the importance of connectivity to support active mussels populations were observed at the reach scale from Addy et al. (2012) and Schwalb et al. (2015), but never at the catchment scale. Fragmentation of stream habitats results in hampered dispersal potential between patches (Brederveld et al., 2011; Jansson et al., 2000).

A good connectivity status between suitable habitat patches depends on the dispersal potential of the host fish. Therefore, the causes for impairment may be: (i) absence of host fish, (ii) unsuitable habitat conditions for the host fish, (iii) habitat fragmentation (i.e. habitat patches that can be potentially colonized are too distant from the potential sources), and (iv) host species habitat fragmentation (i.e. existence of longitudinal barriers). Our approach includes only the third point. The application to more complex situations would require the inclusion of habitat suitability models for the host fish (see Guse et al., 2015 for fish habitat modeling with EMCs) and extending the connectivity assessment to include migration barriers (see Erős et al., 2018 for a connectivity-based analysis of longitudinal migration barriers). However, while datasets on existing barriers are usually available, information on the relative passability is hard to estimate and may greatly affect the results (Buddendorf et al., 2019). Nevertheless, our approach highlights that few strategic habitat patches are responsible for most of the catchment connectivity, allowing for a prioritization for conservation.

4.5. Integrative assessment for the Aist catchment

Dispersal potential, habitat quality, and ARI are not correlated quantities, and therefore suitable as complementary information in the multi-life stage assessment. Our integrative approach makes the main problem for the FPM population in the Aist system obvious: sites where all three indicators that are relevant for the whole life cycle of the species are in a favorable state, are largely lacking (Fig. 6). Therefore, our approach shows on one hand the urgency for conservation action as well as provides a tool for systematic

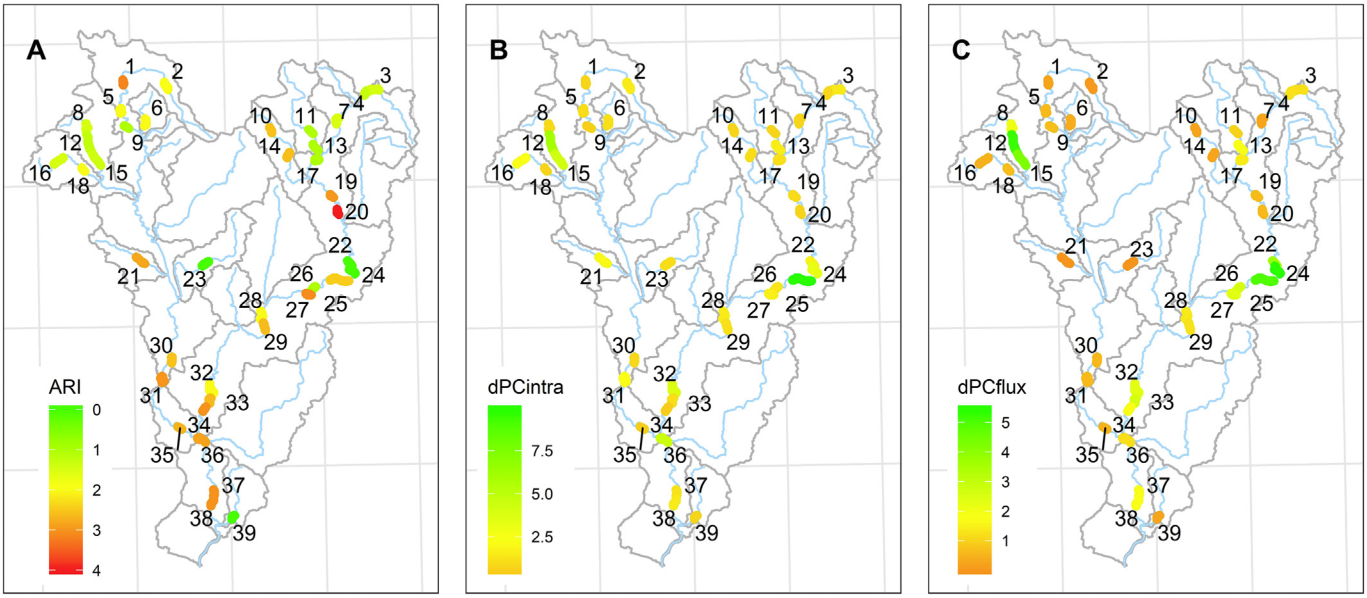

Fig. 5. A) Accumulation risk index, B) dPCintra, C) dPCflux. In each of these images, numbers represent patches identification. The yellow in the scale represents the mean value of the indices; green values are sites that are more important than the average, red values are sites that are less important than the average.

conservation planning, as it can be used as a basis to develop patch specific restoration options:

- Conservation measures could include support populations via augmentation, reintroduction, and relocation efforts (Hoftyzer et al., 2008) in those sites that are suitable for adult and juvenile and offering the highest potential for dispersal (Schwalb et al., 2011; e.g. habitat patch 15 in Figs. 5, 6).
- Habitats that are important for catchment connectivity but have reduced suitability for adult and juvenile stage should also be targeted for hydromorphological modifications to increase the stream transport capacity for those sections that are saturated with sediments

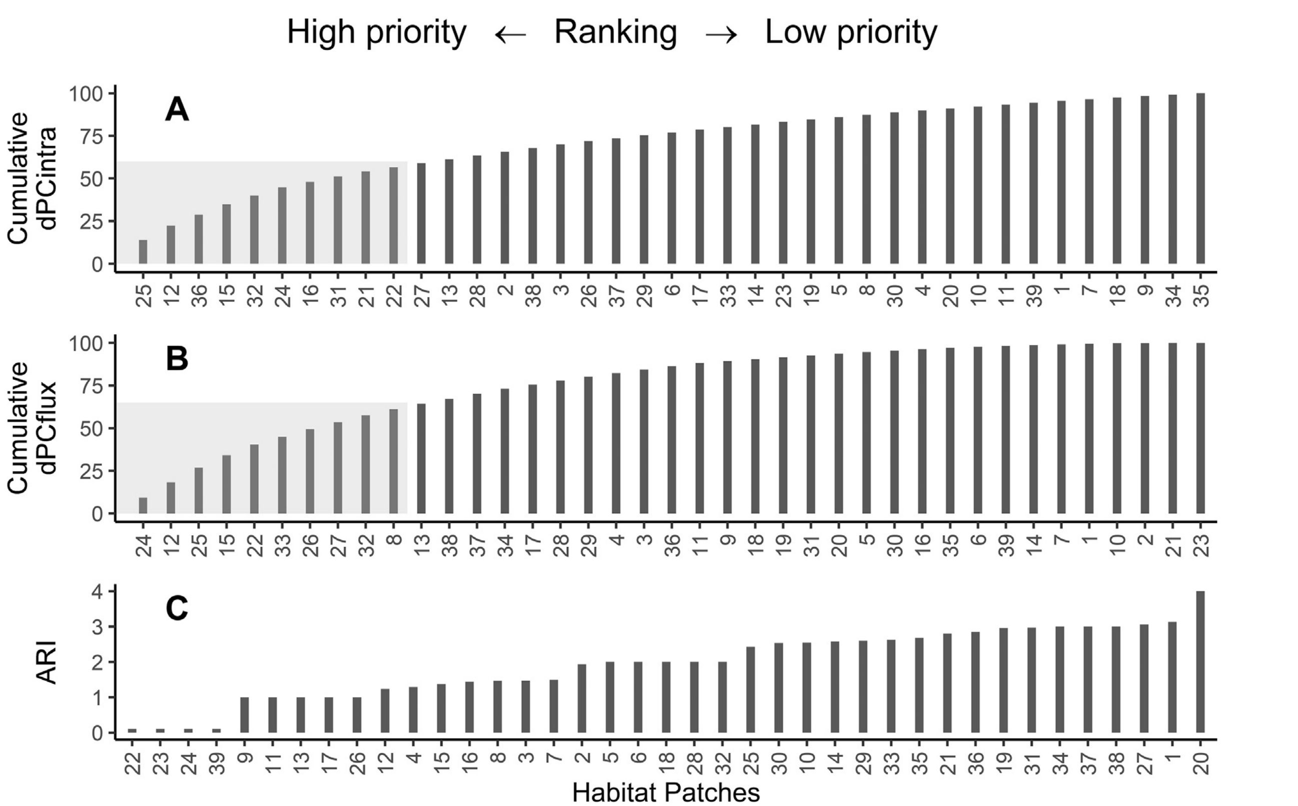

Fig. 6. A) cumulative contributions of single habitat patch to dPCintra indices; B) cumulative contributions of single habitat patches to dPCflux indices; C) Accumulation risk index for single habitat patches. In all figures, patches with good indices values are on the left side. The grey boxes represent patches that are particularly important for adults and glochidia. Numbers in the horizontal axis refer to habitat patches. See Fig. 5 for the position of patches in the Aist catchment.

(Naden et al., 2016) or to increase the channel stability for those sections that are not impacted by fine sediment accumulation (e.g. habitat patch 24). When properly designed, cross sectional modifications can support the achievement of stable conditions for adult mussels and prevent increased sand deposition causing clogging of the substrate for juveniles (Hauer, 2015).
- Sites characterized by high sediment accumulation risk and offering both high habitat quality and connectivity potential can benefit from additional structural measures targeting sediment generation and transport. Structural measures such as vegetated buffer strips and sediment retention areas can be useful to stop the sediment fluxes before they enter the stream (Betrie et al., 2011; Strauch et al., 2013; Ullrich and Volk, 2009). In-stream sedimentation basins can be located strategically in the tributaries that are responsible for the highest sediment loads and at the same time are not providing potentially suitable habitats (Kondolf et al., 2014; Verstraeten and Poesen, 2000; e.g. habitat patch 25).

5. Conclusion

This paper describes a novel integrated modeling framework for the identification and prioritization of sites for Freshwater Pearl Mussel conservation including the assessment of connectivity and the impact of a major pressure for habitat impairment (fine sediment accumulation). The model interlinkage was successful and provided insights into the major drivers for sediment accumulation and the habitat niches for different life stages of the Freshwater Pearl Mussel. If data are available for other systems, the presented framework can be transferred to other catchments, regions, countries, pressures, and organisms. The proposed framework can be used to explore the cascading effects of multiple local and global pressures on hydrological, hydraulic, sedimentological, habitat, and connectivity patterns to develop adaptive conservation plans (Inoue and Berg, 2017; Strayer and Dudgeon, 2010).

CRediT authorship contribution statement

Damiano Baldan: Conceptualization, Methodology, Data curation, Software, Formal analysis, Validation, Visualization, Writing - original draft, Writing - review & editing. **Mikolaj Piniewski:** Validation, Methodology, Writing - review & editing. **Andrea Funk:** Software, Validation, Methodology, Writing - review & editing. **Clemens Gumpinger:** Data curation, Writing - review & editing. **Peter Flödl:** Software, Validation, Writing - review & editing. **Sarah Höfer:** Data curation. **Christoph Hauer:** Software, Validation, Supervision, Writing - review & editing. **Thomas Hein:** Conceptualization, Methodology, Supervision, Writing - review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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