



Social equity shapes zone-selection: Balancing aquatic biodiversity conservation and ecosystem services delivery in the transboundary Danube River Basin



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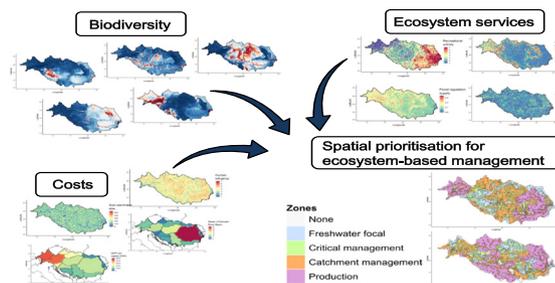
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HIGHLIGHTS

- We illustrate ecosystem-based management in the transboundary Danube River Basin.
- We optimised biodiversity and ecosystem services across countries in the Danube Basin.
- Social equity may entail that wealthy countries pay more for conservation.
- We included social equity as a cost, reflecting countries' wealth and basin share.
- Our generic framework can be applied and extended to other realms and regions.

GRAPHICAL ABSTRACT



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ABSTRACT

Freshwater biodiversity is declining, despite national and international efforts to manage and protect freshwater ecosystems. Ecosystem-based management (EBM) has been proposed as an approach that could more efficiently and adaptively balance ecological and societal needs. However, this raises the question of how social and ecological objectives can be included in an integrated management plan. Here, we present a generic model-coupling framework tailored to address this question for freshwater ecosystems, using three components: biodiversity, ecosystem services (ESS), and a spatial prioritisation that aims to balance the spatial representation of biodiversity and ESS supply and demand. We illustrate this model-coupling approach within the Danube River Basin using the spatially explicit, potential distribution of (i) 85 fish species as a surrogate for biodiversity as modelled using hierarchical Bayesian models, and (ii) four estimated ESS layers

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produced by the Artificial Intelligence for Ecosystem Services (ARIES) platform (with ESS supply defined as carbon storage and flood regulation, and demand specified as recreation and water use). These are then used for (iii) a joint spatial prioritisation of biodiversity and ESS employing Marxan with Zones, laying out the spatial representation of multiple management zones. Given the transboundary setting of the Danube River Basin, we also run comparative analyses including the country-level purchasing power parity (PPP)-adjusted gross domestic product (GDP) and each country's percent cover of the total basin area as potential cost factors, illustrating a scheme for balancing the share of establishing specific zones among countries. We demonstrate how emphasizing various biodiversity or ESS targets in an EBM model-coupling framework can be used to cost-effectively test various spatially explicit management options across a multi-national case study. We further discuss possible limitations, future developments, and requirements for effectively managing a balance between biodiversity and ESS supply and demand in freshwater ecosystems.

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1. Introduction

In light of the strong anthropogenic pressures faced by freshwater ecosystems, such as habitat degradation, pollution, flow regulation and water extraction, freshwater biodiversity is currently facing a crisis with observed population declines for many species (Ricciardi and Rasmussen, 1999; Loh et al., 2005; Dudgeon et al., 2006). Given both the growing awareness of the importance of ecosystem services (ESS) provided by freshwater ecosystems (Aylward et al., 2005) and their ineffective protection (Dudgeon et al., 2006), there is increasing recognition that new management schemes are required for safeguarding freshwater ecosystems and the ESS they deliver to people. For instance, the European Union has committed to designing a network of green and blue infrastructure (Maes et al., 2012), highlighting the policy application when assessing the balance of biodiversity and ESS.

One such management scheme is Ecosystem-Based Management (EBM), with its central principle to concurrently consider biodiversity and human society as integral parts of the ecosystem (Long et al., 2015; Langhans et al., in press). The key goal of EBM is to protect and restore ecosystem resilience, while maintaining biodiversity and the provision of ESS. EBM principles were developed in the 1970s (Caldwell, 1970), but moving from their conceptual to practical implementations has been a major challenge (Slocumbe, 1993; Leslie and McLeod, 2007). While the concept of EBM has a long tradition in terrestrial (Slocumbe, 1993) and marine realms (Botsford et al., 1997), EBM in freshwater systems has been targeted somewhat more recently (Falkenmark, 2003). The complexity of developing EBM measures for freshwater ecosystems can be exemplified by looking, for instance, at Europe's second longest river, the Danube. The Danube comprises a highly stressed and highly vulnerable system given its high level of socio-economic usage (Hein et al., 2018). The high use of ESS, especially in a transboundary setting with 19 involved countries whose demands partially conflict (Sommerwerk et al., 2010; Hein et al., 2018), can carry potentially high costs for biodiversity (e.g., navigation and locks have likely detrimental effects on fish migration). However, because ESS are partly based on biodiversity itself (e.g., food webs and food security, or recreation potential and aesthetic value), the value to society of protecting biodiversity should be evident, particularly as science identifies and demonstrates these linkages (Mace et al., 2012).

This raises two questions: (1) how a balance between biodiversity and ESS could be achieved (Martínez-Fernández et al., 2014), and more importantly, (2) could such a balance be tested (or simulated) in any given area of interest? A first general and useful approximation can be achieved, for instance, using linkage frameworks (similar to e.g., the Driver–Pressure–State–Impact–Response, DPSIR framework; EEA, 1999). As shown by Knights et al. (2013) in the marine

realm, management measures can be achieved by assessing ecosystem complexity and evaluating impact chains across multiple marine sectors and activities. Such an approach can help provide an overall picture of possible management options, for example, regarding sustainable fisheries. Linkage frameworks, however, lack the spatial aspect that is crucial in riverine systems given their longitudinal connectivity. This is especially true for transboundary river basins such as the Danube, where the locations of specific protection or management actions are important from a multi-national management perspective.

Recently, Langhans et al. (in press) reviewed the requirements for a successful EBM planning process, and highlighted several needed components: knowledge of biodiversity, ESS, and deficits in reaching their targets, plus external scenarios, management strategies and spatial planning, with the outcome being a spatial optimisation plan that informs EBM implementation. The authors laid out the theory behind a workflow consisting of three elements: the spatial representation of (i) biodiversity, (ii) ESS, and (iii) the concurrent spatial prioritisation of biodiversity and ESS supply and demand. Langhans et al. (in press) propose three versions of this workflow, which they term “ultralight”, “light” and “full” versions. The **ultralight** version considers the spatial representation of the three elements at the present time step. Beside evaluating the status quo, it allows the user to test how biodiversity and ESS could be balanced by management zones *sensu* Abell et al. (2007), given specific management targets (Fig. 1). The **light** workflow adds complexity to the ultralight one by considering different management strategies that are evaluated and ranked according to relevant criteria, such as proximity to management targets, deficits in achieving biodiversity and ESS targets, and evaluating effectiveness, efficiency, and social equity of management scenarios. Here, effectiveness refers to which degree management impacts the ecological outcomes, whereas efficiency refers to the benefit-to-cost ratio. Social equity, in turn, refers to the fair treatment of individuals or groups (Langhans et al., in press). Finally, the **full** workflow adds data-driven scenarios (e.g., potential alterations in biodiversity and ESS under climate or land use change impacts) to the light version, allowing for detailed estimates of how and where spatial biodiversity and ESS management zones could be planned. As opposed to a binary “protect vs. non-protect” scheme when laying out reserve network plans (Margules and Pressey, 2000), zones with varying intensities of conservation and anthropogenic use decrease the area required for strict conservation, while still meeting species protection targets (e.g., by up to 62% as shown by Hermoso et al. (2016) in the Iberian Peninsula). The three versions differ in their complexity, and hence also in their data requirements. While the ultralight workflow can be achieved with data that can be readily developed (spatial biodiversity and ESS estimates), the light and full versions require additional data and information on external

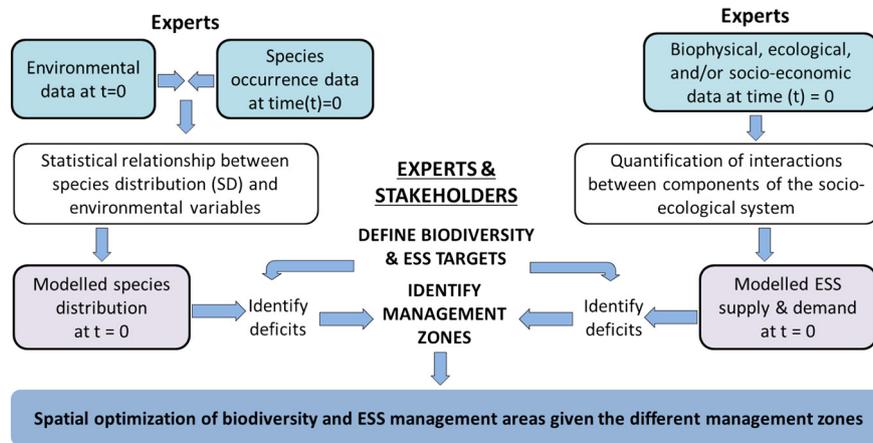


Fig. 1. The 'ultralight' ecosystem-based management (EBM) workflow as proposed by Langhans et al. (in press). The model coupling consists of (i) spatially explicit, range-wide estimates of biodiversity using species distribution models (SDMs, left) and (ii) spatially explicit ecosystem-service models (ESS, right) within a defined study area. The output of these two models is then used to spatially prioritise biodiversity and ESS supply and demand. Source: Figure modified after Langhans et al. (in press).

scenarios, as well as stakeholder involvement (Langhans et al., in press).

Our aim in this paper is to provide a spatially explicit and generic model-coupling framework that can be adapted to virtually any region, following the theoretical workflow proposed by Langhans et al. (in press) and shown in Fig. 1. For demonstration purpose, we illustrate the ultralight workflow, and discuss data requirements and future developments required for light or full applications.

In a first step, we assess the spatial representation of both biodiversity and ESS supply/demand. In a subsequent step, we perform a spatial prioritisation, balancing biodiversity and ESS into different management zones according to user-defined management targets. We illustrate the EBM model-coupling framework for the Danube River Basin. We use the potential distribution of 85 fish species as modelled by spatially explicit Bayesian hierarchical species distribution models as a surrogate for biodiversity. ESS are represented by four layers depicting terrestrial carbon storage and flood regulation supply, and recreation and water use demand, modelled using the ARTificial Intelligence for Ecosystem Services (ARIES) platform (Villa et al., 2014; Martínez-López et al., 2018). We then use the systematic conservation planning software Marxan with Zones (Ball et al., 2009; Watts et al., 2009) to spatially allocate the distribution of biodiversity and ESS into three freshwater conservation management zones defined by Abell et al. (2007): a conservation zone with a strict emphasis on biodiversity protection, a management zone allowing for greater use of ESS, and a critical (buffer) zone allowing for an intermediate use of ESS that simultaneously provides connectivity between conservation zones. We also include a production zone, defined as a zone where increased water use is allowed, while not compromising biodiversity conservation (Hermoso et al., 2018). We further simulate possible multi-national constraints in establishing potential zones for EBM by employing purchasing power parity (PPP)-adjusted gross domestic product (GDP) per capita (i.e., GDP adjusted for differences in relative spending power between different countries that result from different prices for goods) and the relative share of each country's area of the Danube River Basin within the spatial prioritisation.

This proof-of-concept, as demonstrated for the transboundary Danube, aims to highlight how multiple model-coupling elements link to each other. We also discuss further possible extensions and limitations of the approach towards the larger goal of more integrated freshwater management that balances biodiversity and ESS.

2. Material and methods

2.1. Study area

We used the Danube River Basin, draining an area of 807,827 km² (Habersack et al., 2016) as our study area (Fig. 2). We used sub-catchments as conservation planning units in our analyses and extracted all level 12 sub-catchments of the HydroBASIN dataset (Lehner and Grill, 2013) draining into the Black Sea, comprising of 7376 sub-catchments with an average size of 108 km². All planning units were treated as spatially explicit entities throughout the analyses, meaning that the “as-the-fish-swims” connectivity between planning units was integrated in the analyses. Connectivity was specified as a 500 km up- and downstream distance for each planning unit, irrespective of dams, yielding a seamless connectivity matrix across all planning units.

2.2. Biodiversity models

Fish survey data consisted of detection/non-detection information for 85 fish species (Supporting Information Table SI4) derived from the European Fish Index (EFI+) and the BioFresh project databases (Zupancic, 2015; Schinegger et al., 2016), sampled from the years 1955–2007 for the Danube River Basin. Species data, including species detections, non-detections, and sampling dates (i.e., the number of visits per basin) were aggregated to the planning units using the “raster” package in R (Hijmans and van Etten, 2018; R Development Core Team, 2018).

Within each planning unit, we extracted climatic (Hijmans et al., 2005), topographic (Amatulli et al., 2018), land-cover variables (Tuanmu and Jetz, 2014, all at 1 km native spatial resolution) and the number of dams (Lehner et al., 2011) for each sub-catchment, the latter serving as a proxy for hydrologic alteration. We averaged these predictors across planning units, with the exception of the number of dams and precipitation, which we summed across planning units (where the upstream accumulated precipitation along the stream network mimics runoff; Domisch et al., 2015). We omitted highly correlated environmental predictors if Pearson's correlation coefficient $|r| > 0.7$ (Dormann et al., 2013); see Supporting Information Table SI1 for all predictors used). Finally, we centered and scaled

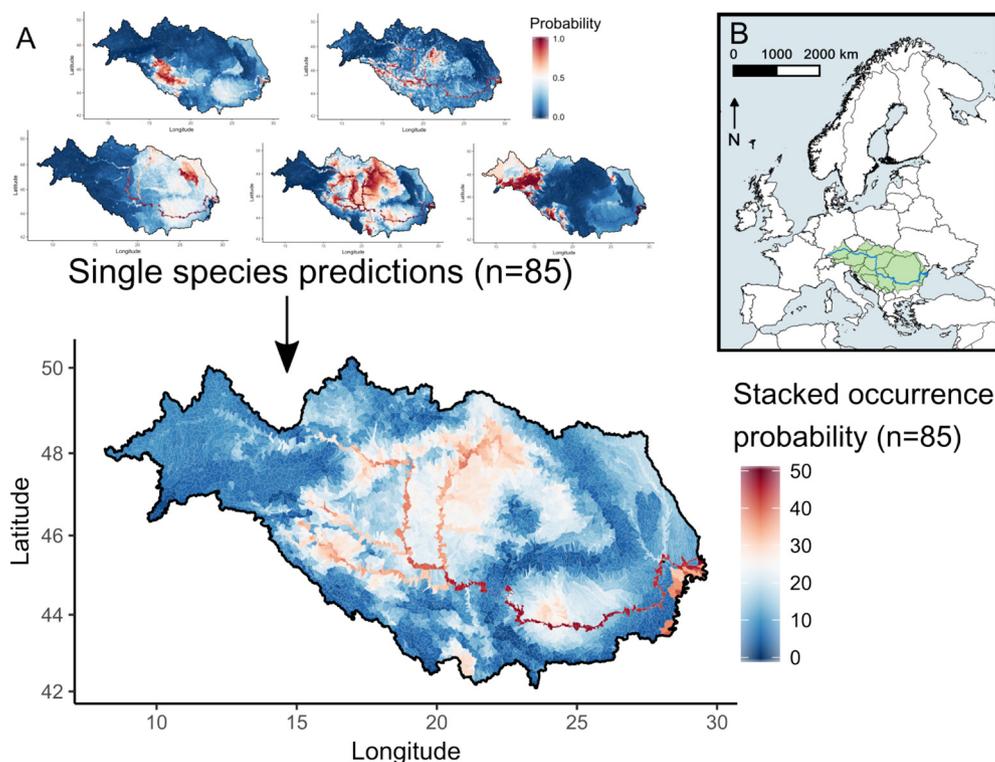


Fig. 2. (A) Example single-species predictions (top), and the summed probability of all 85 fish species distributions in the Danube River Basin (bottom). Summed probability is for illustration only and is not used as such in Marxan with Zones. (B) The location of the Danube River Basin (light green) and the Danube main stem (blue) in Europe. The Danube River Basin outline and main stem shapes were obtained from the International Commission for the Protection of the Danube River (ICPDR).

all eight continuous predictors (i.e., predictors are divided by their standard deviations and have a mean of zero).

We modelled the potential, probabilistic habitat suitability of each fish species within the Danube River Basin using a species distribution model (SDM). In general, a SDM uses species occurrence locations and environmental predictors at those locations to assess the “environmental envelope” of the species, which can then be interpolated using range-wide predictors, yielding a potential habitat suitability map across a study area (Elith and Leathwick, 2009). In this study, we used a hierarchical Bayesian spatially explicit SDM, modelled using the “hSDM” package in R (Vieilledent et al., 2014). This model integrates Bernoulli suitability and Binomial observability processes into a hierarchical zero-inflated binomial model (Vieilledent et al., 2014). The Bernoulli suitability process uses species occurrence records and environmental predictors as the response and explanatory variables. The suitability process is extended using an intrinsic conditional autoregressive model (iCAR), which accounts for the spatial autocorrelation of variation in the occurrence probability of habitat suitability that is not explained by the environmental variables. Since significant spatial autocorrelation was detected for 82 of the 85 species, the use of spatial random effects to account for spatial autocorrelation in the models was warranted (see Domisch et al., 2016 for a full description).

The observability process uses the number of sampling visits within each planning unit to estimate the probability of observing a given species, given the species’ presence in a planning unit. Here, we assume that if the species was observed at least once during multiple visits in a planning unit, the habitat is deemed suitable and the absence of the species during other visits in this planning unit is due to imperfect detection.

We ran three Markov chain Monte Carlo (MCMC) simulations with 200,000 iterations each, a burn-in phase of 50,000 iterations

and a thinning interval of 10. Model convergence was assessed by the multivariate potential scale reduction factor (MPSRF; Brooks and Gelman, 1998). For the suitability process, we used the coefficients from an initial, non-spatial generalized linear model (GLM) as initial values, and both suitability and observability processes used uninformed priors centered at zero with a fixed large variance of 100 (Domisch et al., 2016). The prior distribution for the variance of the spatial random effects followed a uniform distribution, i.e., a flat prior where the upper bound of the variance is set to 10. Species data were split into training (70%) and validation (30%) sets, and model performance for each species was evaluated using the Area Under Curve (AUC), True Skill Statistic (TSS), and sensitivity and specificity (true positive and negative predictions, respectively). Please see the Supporting Information for details on the entire SDM workflow and species predictions.

2.3. Ecosystem service models

We used the Artificial Intelligence for Ecosystem Services (ARIES) platform (Villa et al., 2014) to derive ESS estimates in this study (Fig. 3). ARIES is an open-source technology capable of selecting and running models to quantify and map all aspects of ESS provision and use, including their biophysical generation, flow, and extraction by sinks and beneficiaries (Villa et al., 2014). In this study, we modelled four ESS layers: terrestrial carbon storage, flood regulation supply (both defined as ESS supply layers), recreation activity, and water use (both defined as ESS demand layers). We follow Hermoso et al. (2018) and define terrestrial carbon storage and flood regulation supply (indicative of more natural vegetation in the watershed and riparian zones) as “compatible” with protecting freshwater biodiversity, whereas an extensive recreation and water use are defined

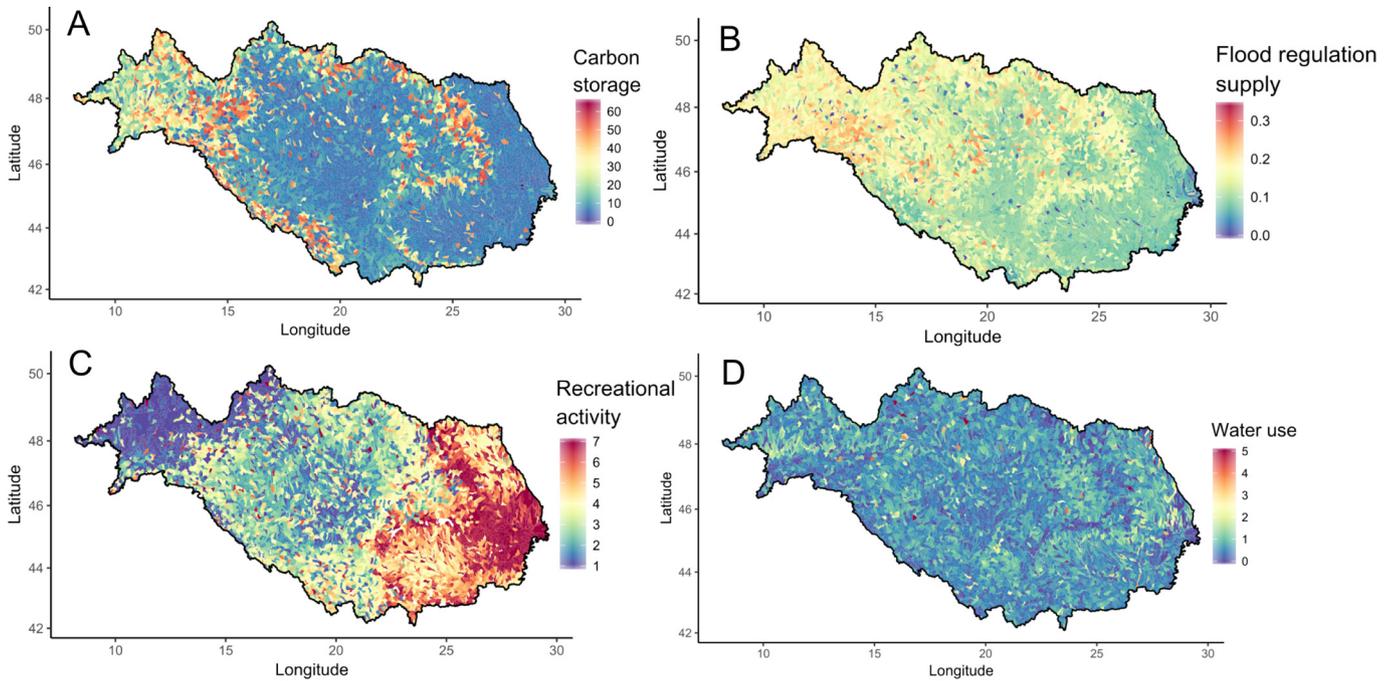


Fig. 3. Four ESS layers used in the model-coupling framework: (A) carbon storage (T/ha), (B) flood regulation supply (relative index), (C) recreational activity (relative index) and (D) water use (relative index). For more details, please see main text and Martínez-López et al. (2018) in this Special Issue.

as “incompatible,” having potential detrimental impacts on biodiversity conservation efforts. All ESS model outputs are produced on a 1 km spatial resolution. We briefly describe each ESS model below and refer to Martínez-López et al. (2018) in this Special Issue for a more detailed description of model structure, assumptions, and data inputs.

The carbon storage model (Fig. 3A) follows the IPCC “Tier 1” methodology developed by Ruesch and Gibbs (2008) and quantifies aboveground and belowground terrestrial carbon storage in vegetation in tons per hectare. The model uses a multi-layer lookup table with land-cover (including wetlands), ecoregion, continent, frontier forests (Potapov et al., 2008), and the occurrence of fire within the last 10 years as inputs (Martínez-López et al., 2018).

The flood regulation model (Fig. 3B) identifies areas providing greater flood regulation as those with higher hazard probability (based on topographic wetness index (Beven and Kirkby, 1979), mean annual precipitation, and mean temperature of the wettest season), and water retention by soils and vegetation, based on the Curve Number (CN) method (Ferrer-Julià, 2003; Soil Conservation Service, 1985). In this study, flood regulation supply is represented as a normalized value between 0 and 1.

The recreation model (Fig. 3C) is inspired by the Ecosystem Services Mapping Tool (ESTIMAP) model of nature-based outdoor recreation developed by Paracchini et al. (2014). Recreation supply is an additive function of naturalness based on land-cover type and the Euclidean distance to nature-based factors of attractiveness (e.g., distance to protected areas, water bodies, or mountain peaks). Recreation demand takes into account the likelihood of taking a day trip to a certain location and the population defining the “catchment area” of that location given a global travel-time dataset (Uchida and Nelson, 2009). This dataset was normalized and discretized into three classes (easily accessible: ≤ 0.25 ; accessible: 0.25 to 0.5; and not accessible > 0.5). The thresholds of these intervals were calibrated by comparing ESTIMAP results with those from ARIES. The model then estimates a relative recreation value ranging from 1 to 7, i.e., low to high.

The water-use model is based on the Corine Land-Cover dataset (EEA, 2012), and uses the expert-derived lookup table from

Burkhard et al. (2012) to reclassify land-cover to derive a water-use index ranging from 0 (low) to 5 (high). The lookup table reflects that water demand is highest in human-dominated land-cover types, with the highest values corresponding to urban, industrial, and commercial areas, as well as for irrigated agriculture, while more near-natural land-cover types are characterized by generally lower levels of water demand. Note that opposed to the SDMs, we do not validate these “Tier 1” ESS models (refer to Martínez-López et al., 2018 for further information).

A small fraction of sub-catchments in Moldavia and Ukraine had missing ESS data (a total of 314 out of 7376 sub-catchments). To avoid the potential omission of these sub-catchments, we used the corresponding ESS information from the surrounding sub-catchments to fill the gaps. We first aggregated each ESS layer from a 1 km to a coarser 10 km spatial resolution, using the average of 10×10 grids (*r.resamp.stats* function in GRASS GIS; Neteler et al., 2012). We then extended these coarse-resolution ESS layers by a radius of 150 km towards the outer boundary of the Danube River Basin (where intersecting grids are averaged using the *r.grow* function). Finally, we extracted these averaged ESS data for those sub-catchments that initially had missing data.

2.4. Spatial prioritisation

We used the conservation planning software “Marxan with Zones” (Ball et al., 2009; Watts et al., 2009) to spatially prioritise biodiversity and ESS within the Danube River Basin. Marxan solves the so-called minimum-set problem by selecting a set of planning units from a larger pool across the study area. Together, the selected planning units build a conservation network within which user-defined targets for each feature (biodiversity or ESS) are covered for the minimum cost (Gómez et al., 2017). Targets are the amount of each feature to be covered (e.g., 20% of each species’ occurrence that needs to be included in the network solution, or 25% of the total provision of a given ESS). Costs need to be defined for each planning unit separately. Costs can, for example, be derived from the extent of land area, resource harvest value, cultural value, or human impact. The

higher the cost for a planning unit, the less likely the given planning unit will be covered as part of the network. The software also allows the user to consider and vary the degree of compactness of the planning unit-network and the importance of meeting each feature target. Resulting spatial plans identified as “best solutions” are those that among all iterations have the lowest objective function value, which is a combination of the costs, the feature penalty and the connectivity penalty (i.e., a penalty if a feature target or connectivity rule are not met in the spatial plan; Ball et al., 2009; Watts et al., 2009).

Marxan with Zones, an extension of Marxan, additionally aims to minimise the overall costs of the zoning plan, while ensuring that the predefined feature targets are met (Watts et al., 2009). Here, we specified four possible zones *sensu* Abell et al. (2007), characterized by different objectives and constraints: a “focal conservation zone”, a “critical management zone” serving as a buffer, a “catchment management zone” that would allow for higher levels of ESS use that are potentially less compatible with protecting biodiversity (i.e., recreation), and a “production” zone where ESS considered incompatible with biodiversity protection are allowed (i.e., water use). Based on the predicted species and ESS distributions (carbon storage and flood regulation as supply, and recreation potential and water use describing demand), we tested various biodiversity and ESS targets distributed across zones to achieve an overview of possible management plans that spatially balance these input features under predefined targets.

For the species predictions, we transformed the predictive posterior mean probability maps from SDMs into a semi-binary scheme using TSS as a threshold (Allouche et al., 2006). All values below the species-specific threshold were converted to zero and values above the threshold retained their original values. This overcomes the problem of inflating the spatial prioritisation for many planning units that have low probabilities of occurrence (e.g., 10 planning units with probabilistic values of 0.1 would equal one planning unit having a value of 1). Simultaneously, this procedure retained the information of varying occurrence probabilities (as recommended by Tulloch et al., 2016) above a certain level of confidence as given by TSS.

We specified the 85 fish species and four ESS types as features for which we could set targets in the spatial prioritisation, since our aim was to balance the spatial representation of both biodiversity and ESS supply and demand (Hermoso et al., 2018). For the species, we set a feature penalty factor (FPF) of 10 for all species, and an overall species protection target of 15% (focal conservation zone), 10% (critical management zone), 5% (catchment management zone), and 0% (production zone, Table 1). This means that, for example, in the focal conservation zone, 15% of each species’ modelled distribution should be covered by this zone. A high FPF of 10 ensures that all species are forced to meet their targets in the spatial plan.

For each of the four ESS, we set a FPF of 1, and a target of summing up to 30% across the four zones (Table 1). The low FPF of 1 allowed us to specify a higher flexibility of each ESS to be included (or omitted) via the target. For instance, extensive recreation nor water use was allowed to occur in focal conservation zones, and this was achieved

by (i) setting high targets for carbon storage and flood regulation supply (i.e., 15% of the current representation), and (ii) a zero target for recreation and water use ESS within this zone.

Marxan with Zones used the identical spatial representation and longitudinal connectivity between planning units as in the species distribution models (see Supporting Information for details). The Boundary Length Modifier (BLM), a dimensionless parameter that defines the level of aggregation of planning units (Ardrón et al., 2008), was calibrated to 0.15 (Supporting Information Fig. S11). Further, we followed Abell et al. (2007) and Hermoso et al. (2018) to specify rules about which zones would be allowed to be allocated next to each other (Supporting Information Table SI2). Doing so limited the possibility to place catchment management zones directly up- or downstream of a focal conservation zone, but enabled the placement of critical management zones as buffers in between. Likewise, we specified a rule that a focal conservation zone should not be placed directly up- or downstream of a production zone, or a planning unit that is not prescribed under any of our management zones, since these areas could be subject to uncertain management.

2.5. Cost factors for the spatial prioritisation

We specified six cost factors to be applied for a planning unit to be considered in a spatial plan (Fig. 4, Supporting Information Table SI3). Costs included (i) the area of the planning unit (Fig. 4A), where larger areas are considered more expensive to be included in a spatial plan (Hermoso et al., 2018), (ii) recreation ESS demand (Fig. 3C), which, in case of extensive use, can be considered partly incompatible with biodiversity, (iii) anthropogenic water use (Fig. 3D) which is considered incompatible with protecting freshwater biodiversity, (iv) a human influence index (Fig. 4B) depicting the naturalness of a given planning unit, (v) national GDP per capita, PPP (Fig. 4C), and (vi) the relative area of each country that falls within the Danube River Basin (Fig. 4D).

Human influence (Fig. 4B) is the degree of naturalness, calculated as a reclassification of land-cover types into relative values ranging from 1 to 7, with higher values representing increasing land use intensity and human influence (Martínez-López et al., 2018). Within Marxan, an area under high human influence (low naturalness) would receive a high penalty if occurring in focal conservation zones, while in critical and catchment management zones, human influence was allowed to some degree. The rationale behind this decision is that a planning unit with a high human influence might not be suitable for conservation, or at least would be very expensive, because it would require purchase and considerable restoration if being devoted to conservation.

The GDP and relative national area in the Danube River Basin (Fig. 4 C–D) allows the implementation of our model-coupling framework in a transboundary setting, where countries with limited financial resources and land area in the Danube River Basin might face additional challenges in financing EBM in the basin. As Marxan tries to minimise the costs in the objective function, it would search for a less-expensive and alternative spatial configuration of management

Table 1

Targets for all features (biodiversity defined as 85 fish species, and four ecosystem services) per management zone used in the spatial prioritisation analysis.

Feature	Management zone targets [%]			
	Focal conservation	Critical management	Catchment management	Production
Biodiversity (85 species)	15	10	5	0
Carbon storage supply	15	10	5	0
Flood regulation supply	15	10	5	0
Recreation demand	0	5	10	15
Water use demand	0	0	0	30

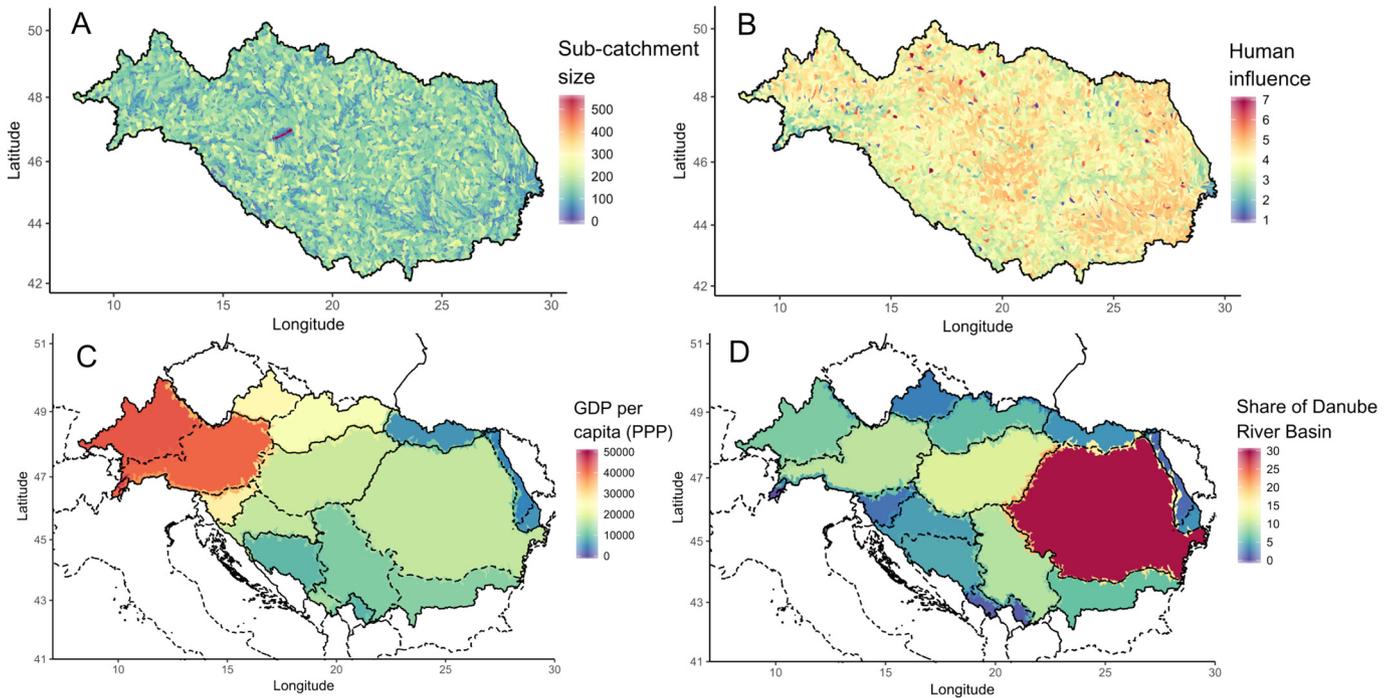


Fig. 4. Four cost layers used in Marxan with Zones: (A) Sub-catchment (planning unit) size in km², (B) human influence, i.e., an index of naturalness, (C) gross domestic product (GDP) using purchasing power parity (PPP), (D) the percent area of each country in the Danube River Basin in km². ESS demand for recreation and water use were used as costs as well (see Fig. 3C–D). Please see main text for further details.

zones given these additional costs. We first extracted the average PPP-adjusted GDP per capita (in 2011 U.S. dollar values) at a 5 degree resolution for the year 2015 (Kummu et al., 2018) for all countries within the Danube River Basin (GADM, 2018). The gridded information was preferred over the overall national information as it takes the possible county-level variability in GDP into account. We then averaged GDP for each country across those areas that intersect with the Danube River Basin and transferred the average national GDP to each planning unit. If a planning unit intersected with several countries, we used the average GDP among these. We then applied an inverse GDP per planning unit as a cost along with a zone-specific multiplier: a country with a low GDP is assumed to have (i) limited resources to allocate focal conservation zones, and (ii) a high interest in financially profitable production zones (high water demand). Inverse GDP is needed so that Marxan with Zones applies a high cost in selecting focal conservation zones in these countries, hence trying to reduce the likelihood of their inclusion in the spatial plan. We did not intend to override biodiversity conservation in spatial plans, but to demonstrate how administrative and national financial constraints can be at least partially included in the spatial conservation planning.

The GDP and relative area per country metrics can have a strong influence on spatial plans, as country borders might stand out as zone borders as well. To avoid undermining the influence of longitudinal connectivity, we balanced the weights for GDP and relative area with those for BLM. This yielded a stronger relative influence of longitudinal connectivity on the spatial allocation of zones, while still accounting for macro-scale patterns of GDP and relative area within the Danube River Basin. All costs were scaled from 1 to 100 to enable their direct comparison and to facilitate calibration of cost parameters.

We acknowledge that we met these simplified assumptions for illustrating the model-coupling approach using a blank-slate example with a high level of flexibility to simulate different settings

in the spatial prioritisation. For simplicity, we refrained from locking in any current, already established protected areas in the spatial plan. The inclusion of established protected areas decreases this flexibility. Additionally, current protected areas have not necessarily been optimised considering the 85 fish species we use as targets. They have generally rarely considered freshwater biodiversity, but have been established regarding multiple (terrestrial) species groups, biodiversity indices such as species richness, or land-cover types as surrogates, in combination with financial constraints (Ardron et al., 2008). An overview of the water-related protected areas of the Danube River Basin is provided in the river basin management plan (ICPDR, 2009b). We also assumed equal production intensities and management expenses for maintaining different zones across countries.

2.6. Spatial prioritisation using Marxan with Zones

We ran two spatial prioritisation analyses with the above settings (see Table 1 for a description of the targets). We kept the targets for all features fixed (summing to 30% across zones). First, we applied the following costs: sub-catchment area, human influence, recreation, and water use (see Supporting Information Table S13). We then compared the results of this “basic” analysis with a new spatial prioritisation, in which we additionally employed national-level costs via GDP and the relative share in area per country in the Danube River Basin (referred to as “GDP-area” analysis). We aimed to show how EBM plans across the Danube River Basin could change if we assume an equal share of costs among all the involved countries compared to a multi-national EBM plan given potential national-scale financial constraints. This would also include the assumption that countries with a lower percentage of their area in the basin would devote less to EBM planning than those countries that largely fall within the basin. For both analyses, we ran 100 repetitions with

1,000,000 iterations each. We report the total area per zone, the average $\pm SD$ of the GDP and area-within-basin within each zone.

3. Results

3.1. Biodiversity and ESS models

Model validation of SDMs yielded high evaluation scores across all 85 species (Supporting Information Table S14), with $AUC = 0.892 \pm 0.081$ (average $\pm SD$, sensitivity = 89 ± 11.39 , specificity = 82.73 ± 10.91 , TSS = 0.722 ± 0.152 , and a detection probability of 0.33 ± 0.24). Fig. 2 shows example maps of single-species predictions, and stacked occurrence probabilities to illustrate the estimated richness pattern of those 85 fish species. The stacked occurrence probability (as a proxy for richness; Mateo et al., 2012) increased from the Upper towards the Lower Danube, including the tributaries Drava, Sava, and Tisa, and further towards the Danube Delta (Fig. 2).

Regarding the ESS models, greater areas of carbon storage are evident in forested areas of the Carpathian Mountains, the Dinaric Alps, and the Alps that form the western headwaters of the Danube River (Fig. 3A). Similarly, areas of greater flood regulation are evident on these and other areas with greater natural land-cover (Fig. 3B). Recreational activity (Fig. 3C) follows a gradient from the Upper to the Lower Danube, with high recreational activity areas in the Carpathian Mountains and the Danube Delta area. High water-use areas coincide with the location of urban, industrial, commercial, and irrigated agriculture areas (Fig. 3D).

3.2. Spatial prioritisation

The best solutions among the 100 repetitions for both “basic” and “GDP-area” runs showed that all feature targets were achieved for biodiversity and ESS (Fig. 5 A–B). In reaching the best solution in the basic analysis, the total area allocated to catchment management ($283,520 \text{ km}^2$) was double that of focal conservation ($136,888 \text{ km}^2$), while requiring $222,437 \text{ km}^2$ for fulfilling the production zone target (Fig. 6A). In the GDP-area analysis, fulfilling the targets required $120,407 \text{ km}^2$ to be considered as a focal conservation zone, with $296,189 \text{ km}^2$ allocated to production zones. Out of $807,827 \text{ km}^2$, $30,111 \text{ km}^2$ were not allocated to any management zone.

Predefining costs and weights for GDP and percent area within the Danube River Basin (Supporting Information Table S13) led to a different spatial representation of the four management zones in the best solutions (Fig. 5 A–B). These effects were also mirrored in the average GDP per zone (Fig. 6B) and the percent area of each country of the Danube River Basin (Fig. 6C). Compared to the basic analysis, the best solution derived from the GDP-area analysis (i) left a fraction of planning units outside the designated management zones, (ii) and planning units of the focal conservation, critical management, and catchment management zones would be located in countries with a higher GDP, as well as in countries that have a higher percentage of their area within the Danube River Basin (Fig. 6 B–C).

4. Discussion

Ecosystem-based management (EBM) is considered to derive effective and sustainable management options for freshwater biodiversity, while concurrently considering the needs of biodiversity and human society (Long et al., 2015; Langhans et al., in press). We followed the work of Abell et al. (2007) and Hermoso et al. (2018), and integrated the spatial planning framework into the conceptual framework proposed by Langhans et al. (in press). We demonstrate this framework by applying the “ultralight” workflow (Fig. 1) within the transboundary Danube River Basin. The model-coupling process consists of first quantifying the current spatial representation

of biodiversity and ESS, followed by setting management targets for distinct management zones. We then used a spatial prioritisation to allocate management zones across the sub-catchments (i.e., planning units) within the Danube River Basin, fulfilling biodiversity and ESS targets, while minimising the costs associated with the spatial plan. By specifying the spatial dependencies between planning units, we accounted for longitudinal connectivity within management zones, including buffer zones between conservation management and production zones.

The basic and GDP-area analyses led to clear differences in the spatial configuration of management zones. Interestingly, a reasonable target of 1/3 of each feature could be reached even with (simulated) national constraining costs, i.e., where high-GDP and high-percent area countries are assumed to devote more resources towards conservation than their counterparts.

In the GDP-area analysis, we gave an *a priori* priority to focal conservation zones and critical management zones to be allocated within high-GDP countries, and countries that cover a larger fraction of the river basin (expressed using the costs). This evoked a change in zone allocation, e.g., in the Upper Danube, where production- and catchment management-dominated zones in the basic analysis were replaced by focal conservation, critical and catchment management zones in the GDP-area analysis (Fig. 5 A–B). Given the concept of irreplaceability, this means that these areas contain predictions of those fish species that are not unique in the Upper Danube, and could be covered by selecting planning units in other areas where the GDP-area costs are lower than in the Upper Danube. Likewise, the compatible ESS features (carbon storage and flood regulation supply) were represented in other areas of the Danube River Basin as well. In contrast, the Lower Danube and the Danube Delta stood out as being irreplaceable in terms of biodiversity, as this area was specified as a focal conservation zone in both analyses. This area, hence, contains planning units in which a unique combination of fish occurrences were predicted, and which could only be covered by the high target provided by focal conservation zones, given the low costs in this area (Fig. 4). Although a high recreational activity index was predicted to occur in the Danube Delta (Fig. 3C), coinciding with the designated focal conservation zones, this ESS was also represented, e.g., in the Carpathian Mountains such that the recreation activity targets were fulfilled by Marxan by selecting other planning units.

In the GDP-area analysis, a fraction of the Danube River Basin was left outside the designated management zones. This indicates that the feature targets were met given a different spatial configuration where this fraction was not required. In other words, the GDP-area costs outweighed the cost regarding the area of the planning units, recreation, water use and the human influence index, and indicates how the spatial configuration of management zones can be modified to reach the preferred spatial distribution of zones.

The practical implementation of the “ultralight” workflow laid out by Langhans et al. (in press) shows on the one hand the feasibility of the approach, while on the other hand, the challenges associated with it. The flexibility is underlined by the spatial prioritisation that cost effectively allows testing various biodiversity and ESS management options in a spatially explicit context (Hermoso et al., 2018). The framework by Langhans et al. (in press) further enables the integration of additional aspects; given its flexibility, we also touch on the “light” workflow by highlighting how the cornerstones of EBM, namely effectiveness, efficiency, and social equity can be taken into account in the spatial plans (Langhans et al., in press). Here, effectiveness of a given spatial plan is directly assessed by comparing how well the feature targets are met. Efficiency, as specified using spatial layers depicting costs (Fig. 4), is adjusted for each management zone. Social equity was specified indirectly in Marxan via the costs to achieve the desired outcome, to account for countries’ differential

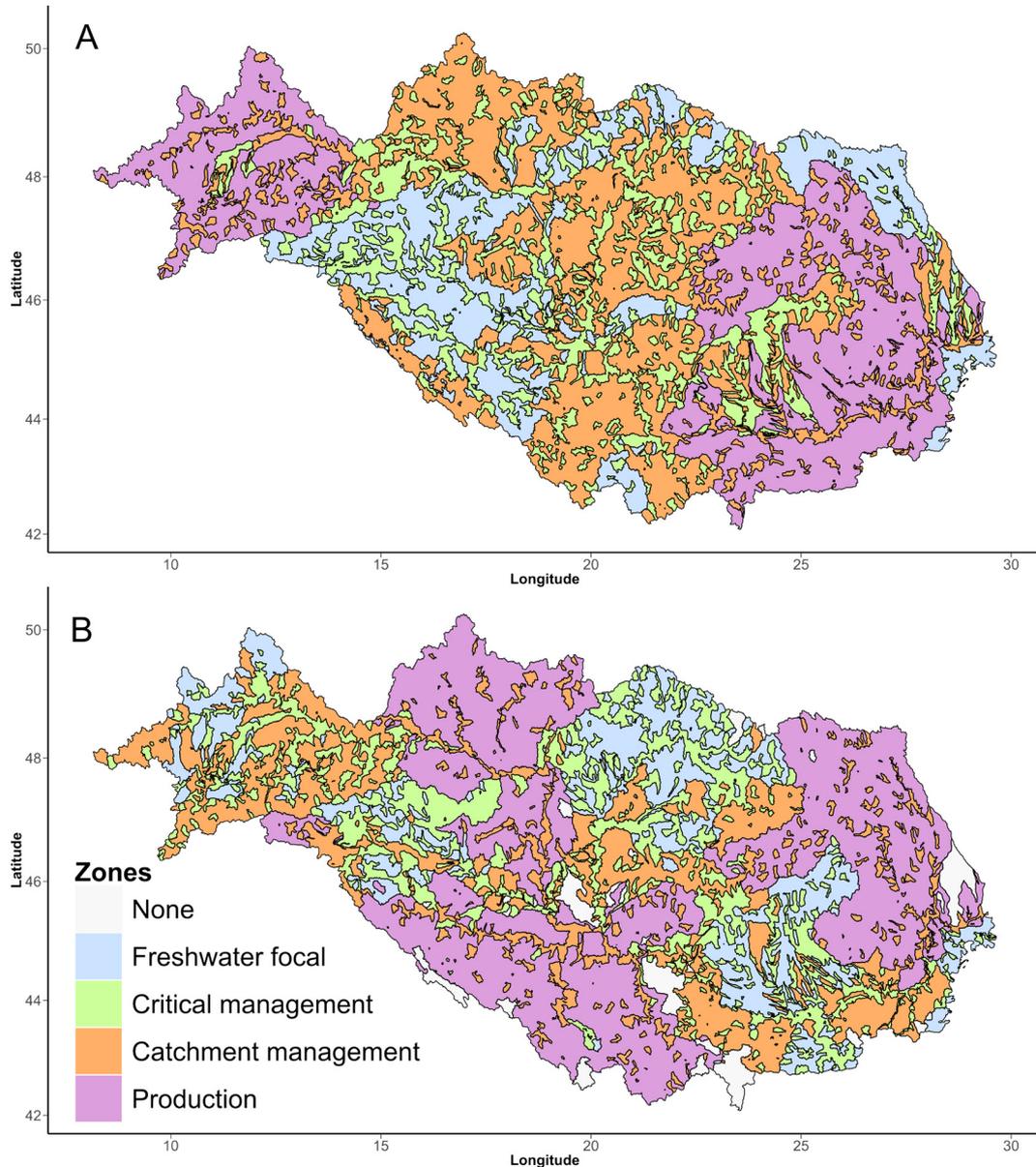


Fig. 5. Spatial prioritisation of biodiversity and ecosystem services (ESS) in the Danube River Basin considering (A) biodiversity and ESS along with the costs of sub-catchment size, human influence, recreation and water demand (basic analysis), and (B) adding the costs of gross domestic product (GDP) per capita (purchasing power parity, PPP) and the portion of each country within the Danube River Basin (GDP-area analysis).

ability to provide the financial resources for EBM. Here, we specified multiple cost factors, including socioeconomic data (Ban and Klein, 2009). We compared the spatial plan derived from an assumption where each country contributes equally to the EBM to one where the PPP-adjusted GDP and the percent area of each country in the basin were used as additional costs.

Considering our two analyses as a demonstration of the ultralight workflow, we acknowledge the hypothetical nature of our study that illustrates the challenges of the approach. Varying targets and costs regarding effectiveness and efficiency are required to yield the optimal spatial representation of management zones in the Danube, along with the spatial configuration of the current protected areas. Moreover, given projected climate and land use impacts on the environment, future potential changes in biodiversity and ESS should be considered in future work (Langhans et al., in press). While the workflow could be further extended as described in Langhans et al. (in press) by ranking management strategies, this would require

external data-driven biodiversity and ESS scenarios to assess possible future EBM management changes.

The “light” and “full” frameworks involve additional aspects for effectively pursuing EBM that are not covered in our example (Langhans et al., in press): (i) modelling biodiversity and ESS across realms (e.g., terrestrial, freshwater, and marine zones), ensuring connectivity and hence accounting for cross-realm dependencies, and (ii) working closely with stakeholders to account for potential scenarios in a given region (e.g., climate or land-use change), as well as to set management strategies. In a real-world situation, targets would additionally (iii) need to take environmental legislation, international agreements, and other policy recommendations into account. Finally, data and model-driven uncertainties should be carefully assessed and communicated throughout the application of the workflow (Hamel and Bryant, 2017).

To inform decision making geared towards successful application of EBM in a way that builds consensus among all countries

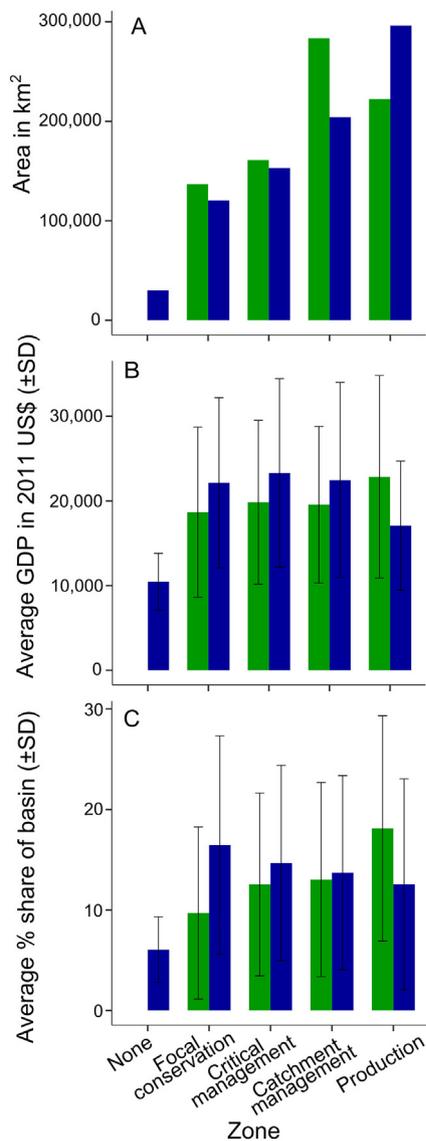


Fig. 6. Barplots representing the best solutions of the two analyses, i.e. using the basic (green) and gross domestic product (GDP)-area analysis (blue): (A) the total area for each zone, (B) the average \pm SD GDP per zone, and (C) the average \pm SD country share within the Danube River Basin per zone. The best solution derived from the basic analysis yielded no planning units outside the management zones.

and stakeholders, while accounting for social equity (Hein et al., 2018), requires that all stakeholders are involved in the spatial planning process during all steps. Further, stakeholder agreement on the biodiversity and ESS data and models, management zone definitions, targets and costs is required. Under these conditions, this model-coupling framework can be used to inform EBM-based decision making. For transnational water bodies, international resource management entities such as the International Commission for the Protection of the Danube River (ICPDR, 2009a) would provide a platform to foster such discussions and facilitate agreements.

While the species distribution models and ecosystem service models use “hard” data for creating their outputs, the spatial prioritisation (i) relies on modelled outputs from SDM and ESS models, and (ii) can be considered subjective regarding its parameters (as also in the spatial planning literature). Spatial planning requires the accommodation of multiple assumptions to yield a solution closest

to optimum. For instance, while the targets are met, it is crucial that the spatial allocation of the different zones meets expectations and is sensible from both ecological and conservation perspectives (e.g., a focal conservation zone should be located upstream of a catchments management zone, as described by Abell et al., 2007). These connectivity penalty parameter values are specific to each study area and need to be calibrated for each study area again. While this may seem arbitrary, the aim is to yield an output that satisfies multiple relevant criteria (i.e., ecology, management, stakeholder preferences, see also Hermoso et al., 2018).

4.1. Conclusions

This quantitative model-coupling framework for EBM (Langhans et al., in press), here demonstrated for the Danube River Basin, shows how biodiversity and ESS estimates can be jointly simulated in any area of interest, given the requisite data and models. Based on this generic model-coupling workflow, EBM provides an iterative process that can be incorporated, including stakeholder involvement and ultimately scenario development. Within a flexible framework, such simulations can be vital to communicate biodiversity and ESS targets regarding effectiveness, efficiency, and social equity, especially in transboundary regions such as the Danube River Basin. In a wider context, by following a consistent theoretical framework, the model-coupling approach is applicable to virtually any region given the basic requirements of species point occurrences and freely available, global environmental predictors for the SDMs and ESS models that can be calculated in ARIES (Villa et al., 2014; Martínez-López et al., 2018).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2018.11.348>.

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