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Linking biodiversity to ecosystem services supply: Patterns across aquatic ecosystems

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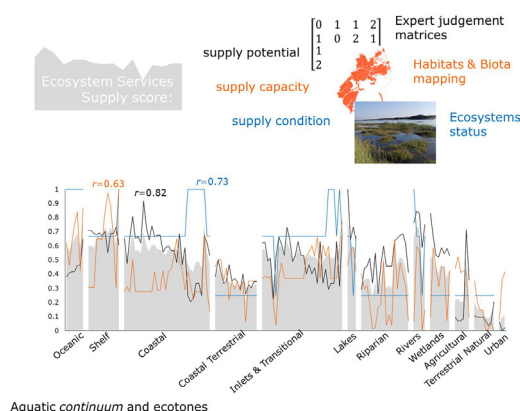
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HIGHLIGHTS

- Comprehensive assessment of aquatic biodiversity links to ecosystem services
- Wide geographical consistency in valuations of aquatic services supply
- Patterns in ecosystem services differ significantly across aquatic systems.
- High complementarity and spatial turnover of services was identified.
- Ecosystem Services Supply score integrates potential, capacity and condition for the freshwaters – marine continuum.

GRAPHICAL ABSTRACT



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ABSTRACT

Global initiatives have been increasingly focusing on mainstreaming the values of biodiversity and ecosystem services into decision-making at all levels. Due to the accelerated rate at which biodiversity is declining and its consequences for the functioning of ecosystems and subsequently, the services they provide, there is need to develop comprehensive assessments of the services and the benefits nature delivers to society. Based on expert evaluation, we identified relevant flow linkages in the supply-side of the socio-ecological system, i.e. from biodiversity to ecosystem services supply for eight case studies across European aquatic ecosystems covering freshwater, transitional, coastal and marine waters realms. Biological mediated services were considered, as well as those reliant on purely physical aspects of the ecosystem, i.e. abiotic outputs, since both have implications for spatial

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planning, management and decision-making. Due to the multidimensional nature of ecosystems and their biodiversity, our approach used ecosystem components such as habitats and biota as proxies for biodiversity and as the focal point for linkage identification. Statistical analysis revealed the importance of considering mobile biota in the spatial assessment of habitats. Contrary to literature evidences so far, our results showed significantly different and complementary ecosystem services supply patterns across the continuum of aquatic realms. The implemented score of ecosystem services supply has a high potential for integrated aquatic ecosystem service supply assessments in the context of ecosystem-based management.

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1. Introduction

Conservation actions require sound knowledge of ecological processes and their interconnections in order to deploy effective and targeted measures. Researchers have been struggling to offer a consistent theory on ecosystem functioning, recognizing that, in all circumstances, ecosystems' complexity needs to be accounted for (Jørgensen et al., 2016). Because of such complexity, the underlying role of biodiversity in ecosystem functioning, its relevance for ecosystem service provision in general, as well as the consequences of its decline, remain poorly understood (Jørgensen and Nielsen, 2013; Kremen, 2005; Laurila-Pant et al., 2015; TEEB, 2010).

Unlike biodiversity to ecosystem functions (BEF) relationships (Daam et al., 2019), there is less established biodiversity to ecosystem services (BES) research (Cardinale et al., 2012). This fact, together with more complex pathways, make it more challenging to demonstrate whether biodiversity has the same pivotal role for ecosystem services (ES) as demonstrated for ecosystem functioning (Harrison et al., 2014; Mitchell et al., 2015). Ecosystem services are generated from numerous interactions occurring in complex ecosystems (Harrison et al., 2014) and biodiversity is expected to have direct and/or indirect effects in ES provisioning. However, whether or not biodiversity benefits from the protection of ES, and vice versa, is valuable scientific knowledge to turn the concept of ecosystem services into a practical conservation tool in the formulation of day-to-day policies at national or regional scales (Ressurreição et al., 2012; Burkhard et al., 2014; Cook et al., 2014; Heink et al., 2016; Mononen et al., 2016). Linkage approaches (Burkhard et al., 2009) are considered effective tools to describe networks of relevant interactions arising from complex social-ecological processes, including those that link biodiversity to ecosystem services. Such links have recently been used to summarise and reveal relevant trends and patterns based on expert judgement or evidences collected from scientific literature (Burkhard et al., 2012, 2014; Campagne and Roche, 2018; Jacobs et al., 2015).

In this study, we used a linkage approach to characterize the potential role of biodiversity in the provision of services across a *continuum* of aquatic ecosystems, from river networks to marine waters. The possibility of identifying the roles of the biotic and abiotic components of ecosystems facilitates the purpose of analysing ecosystem processes in terms of the causal contributions of its parts to an activity of the ecosystem (Jax, 2005), which in the present case is related to services provisioning. Following this rationale, we used such links within an assessment framework (Gómez et al., 2016) to be applied in an ecosystem-based management (EBM) context in aquatic systems. These semi-quantitative assessments can be used for a preliminary screening and mapping of ES potential in data poor regions (e.g. Barbosa et al., 2019), for highlighting potential ES threatened by human activities (e.g. Culhane et al., *this issue*) or for supporting prioritization of stakeholders' ES preferences (e.g. Martínez-López et al., 2019).

Aquatic ecosystems have historically attracted human settlements and their activities, resulting in a long-term exposure to the associated multiple pressures threatening these natural systems (Nöges et al., 2016; Hein et al., 2018; Birk, 2019; Borgwardt et al., 2019). Aquatic

ecosystems have specificities that underline their role in ES provision, but no evidence of differences in services provision between different types of aquatic systems have been found (Boulton et al., 2016). This study considers ES from the supply-side, i.e. the potential and capacity of an ecosystem to supply services, whether or not these are used. Based on estimates from eight case studies from fresh to marine waters and associated land-water ecotones, our goal is to explore BES linkages in aquatic ecosystems.

By integrating biodiversity ecosystem components (habitats and biota) and their associated ecosystem services, our main objectives are i) to investigate the main ES supported by aquatic ecosystems; ii) to reveal patterns in ES supply across different aquatic realms in Europe; and iii) to understand dependencies of aquatic ES on biodiversity, identifying relevant pathways from aquatic systems and associated ecotones to specific services.

2. Methodology

2.1. Case studies

This work is based on contributions from eight case studies (CS) across diverse aquatic domains from fresh to marine waters covering a total area of 612,110 km² in Europe and 3838 km² in Morocco (Borgwardt et al., 2019; Culhane et al., *this issue*). Four case studies had a fully freshwater scope (Danube River - DR, Lough Erne - LE, Lake Ringsjön - LR, and Swiss Plateau - SwP, see Kuemmerlen et al., 2019), another two had a full coastal and marine focus (North Sea - NS, see Piet et al., 2019 and Azores - MPA AZ), while the remaining two CSs encompassed a gradient of aquatic realms from fresh to marine waters (Intercontinental Biosphere Reserve of the Mediterranean - IBRM, see Barbosa et al., 2019 and Ria Aveiro N2000 site - Rav, see Lillebø et al., 2019) (Fig. 1). In addition to aquatic and associated realms, other land cover types (terrestrial) in the vicinity of them were also identified (Fig. 1). Besides the geographical differences, the CS differ also in respect to their size, with areas ranging from 48 km² (LE) to 547,224 km² (NS) (Fig. 1). Such a wide range of systems, in terms of geographic cover and spatial scale, allows testing whether patterns in the supply of ecosystem services change over such gradients or not. Furthermore, each CS is unique in that its socio-ecological context is very diverse (supplementary online material SOM 1), with distinct levels of human activities and pressures (see Borgwardt et al., 2019) and of environmental protection extent and status (see Culhane et al., *this issue*).

2.2. Linkage framework and baseline data

A linkage framework approach was used to characterize the eight studied socio-ecological systems. Prior to establishing meaningful relationship links, a categorisation of ecosystem components (EC) within aquatic realms was undertaken, along with the identification of a suitable ecosystem services (ES) classification. These two typologies were the basis of the linkage framework developed, where the direct links established between them were used to build weighted habitat-service matrices. The analysis of the linkage matrices aimed at

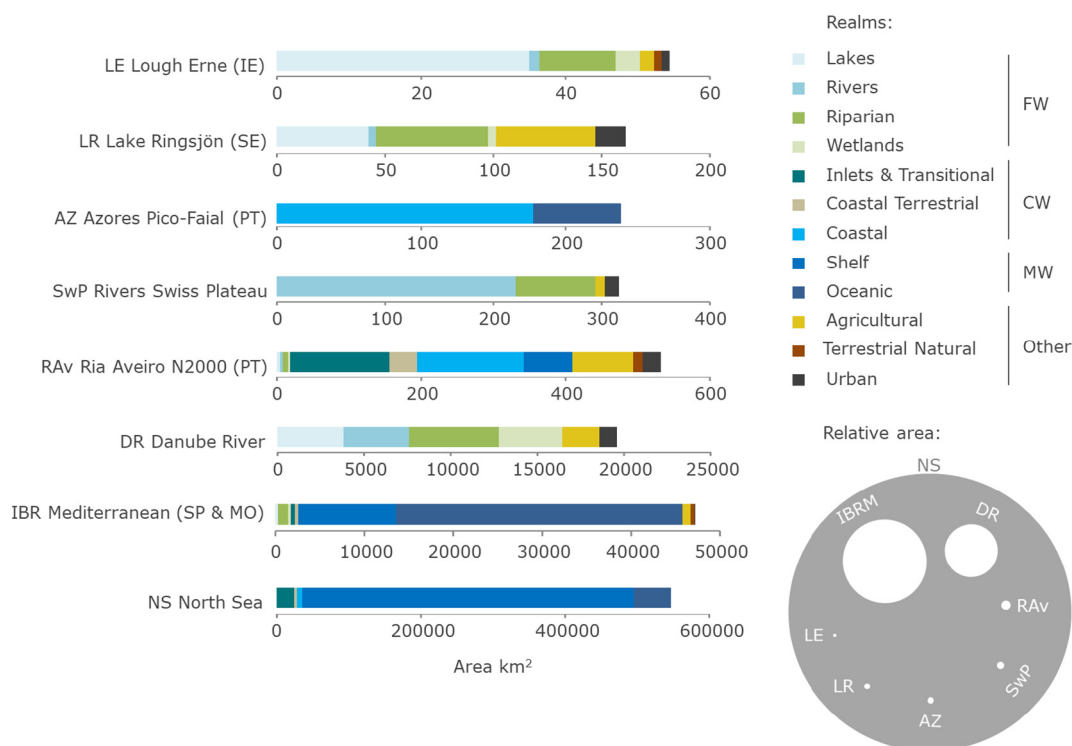


Fig. 1. Realms in four main domains: freshwaters (FW), coastal waters (CW), marine waters (MW) and other non-aquatic, identified in each CS according to typology defined in this study (SOM S1). The area (km²) occupied by each realm in the CS is plotted. Case studies relative area is shown as circles.

unravelling the links between biodiversity and ecosystem services across freshwater and marine environments.

Biodiversity was thus considered by taking its most relevant EC as proxies, i.e. the habitats and most relevant biotic groups identified at site. Habitat mapping in the eight CS used a hierarchic classification at different spatial scales: from domain, to realm, to habitat. Three main domains were defined in a *continuum* from freshwaters (FW), to coastal waters (CW) and to marine waters (MW). An additional fourth domain was considered for other (O) habitats within or adjacent to the main aquatic domains. The domains considered in this study included diverse habitats that have been grouped into 12 realms according to their specificities (Fig. 1; SOM 1 Table S1): freshwaters included the realms of lakes, rivers, wetlands and riparian habitats; coastal waters included inlets and transitional waters, coastal waters, and coastal terrestrial habitats; marine waters included shelf and oceanic waters; and in the other domain, terrestrial natural habitats, agricultural areas, and urban settlements have been considered.

By extending the diversity of assessed realms beyond purely aquatic ecosystems, the role of ecotones (freshwater-terrestrial, freshwater-marine, marine-terrestrial) as ES providers can be understood better. The riparian realm was defined following Weissteiner et al. (2016), and mapped using the Actual Riparian Zones (ARZ) of the Riparian Zones Delineation product by Copernicus (EEA). This information was improved with local data for riparian zone delineation in smaller streams (Strahler's streams order 1 and 2), not covered by the Copernicus product.

The European Nature Information System (EUNIS, 2012) habitat classification from the European Environment Agency (EEA) is widely used in Europe and is applicable across all domains. For this reason, it was adopted to ensure a harmonized characterization of habitats across realms and CS (SOM 1 Table S2). The habitats were described up to EUNIS level 3 resolution whenever possible (SOM 2 Table S3). The highest resolution most commonly available for habitat description across the CS was EUNIS 3 level, with 104 unique realm/habitat pairs reported. For 37 realm/habitat pairs a description was only available at EUNIS 2 resolution, and there were seven realm/habitat pairs reported

at EUNIS 1 resolution. In this study we considered therefore 148 unique habitats, hereafter defined as 'habitat assessment units'.

The area (km²) occupied by each realm in the CS was compiled (Fig. 1), along with the range of cover (in percentage) of each habitat within its respective realm (Table 1). This allowed for an estimation of the habitats' area (km²), by considering the mid-range of the % covered of each habitat (Table 1) to derive habitat area from the respective realm's area.

In addition, highly mobile biota that are not specifically associated with a single habitat or that have dependencies on different habitats through their life cycle were separately considered. This aimed at facilitating the identification of ES specifically associated with the following six mobile biotic groups: insects (adults); fish and cephalopods; mammals; amphibian; reptiles and birds.

To provide a comprehensive ecosystem service assessment, this study included both the services dependent on biodiversity (i.e. biologically mediated) as well as those reliant on physical aspects of the ecosystem (i.e. abiotic outputs, AbO). As both can have implications for spatial planning, their inclusion is crucial for effective management

Table 1

Ranges classes used for reporting habitat relative occupation within realm per CS and correspondent mid-range of class percentage used for estimating the area of each habitat assessment unit (n = 149) in this study.

Habitat cover within realm per CS (% range classes)	Mid-range of scale (%)
Absent	0
[0%–1%] cover	0.5
[1%–5%] cover	3
[5%–15%] cover	10
[15%–30%] cover	22.5
[30%–50%] cover	40
[50%–70%] cover	60
[70%–85%] cover	77.5
[85%–95%] cover	90
[95%–99%] cover	97
[99%–100%] cover	99.5

and decision-making (Armstrong et al., 2012; Kandziora et al., 2013; Lillebø et al., 2016; Sousa et al., 2016). This study considers those services that habitats and/or biotic components provide, whether or not they are used. The classification used in this study was selected to ensure consistency with the Common International Classification of Ecosystem Services CICES (Haines-Young and Potschin, 2013; CICES V5.1); where services are divided into 1) provisioning (P), 2) regulation & maintenance (R&M), and 3) cultural (C). In this study, 33 types of ES are treated at the CICES group level equivalent (SOM 1 Table S4). As an example of the detail at group level: if we consider ecosystem services under the section 'Provisioning' and more specifically within the 'Energy' division, 'Mechanical energy' would represent a service at the group level characterization.

2.3. Expert elicitation of ecosystem service linkages

A structured three-phase elicitation procedure was conducted for identifying linkages between the ecosystem components (EC), which comprise both habitats and biota, and ecosystem services (ES). Linkages were assessed by expert judgement in seven out of the eight CS, involving researchers from the respective CS.

The expert judgement assignments followed a bottom-up approach and assumed a sound local knowledge of the experts on the respective CS, where they identified and weighted the relevant links (available online [AquaLinks dataset, 2018](#)). Multidisciplinary teams of experienced researchers from complementary environmental fields have been involved in the elicitation process, their area of expertise comprising ecology, biogeography, ecosystem services, environmental chemistry, ecotoxicology, spatial planning, conservation and management. A minimum of two experts per CS participated in each round of the elicitation process and it was ensured that at least one person per CS was thoroughly familiar with the system. In order to promote consistency across experts and CS, realms and geographies, a common understanding of ES categories was provided, supported by examples specifically addressing aquatic habitats and related ecotones (SOM 1 Table S4).

It is expected that ecosystem services provided or supported by habitats that occur across a wide range of aquatic environments, may differ accordingly. This is easily perceived, for example, for sublittoral sediment benthic habitats (EUNIS A5) occurring in estuarine systems in comparison to those in deeper open waters. In this sense, although a EUNIS habitat category may be shared across realms, and even domains (SOM 1 Table S2), the link evaluation (identification of relevant links and valuation of the strength of those links) was done for habitats within the context of the individual realms.

The expert elicitation process was conducted in two stages, followed by a final round for revision and consistency check. The methodology followed a process based on iteration and feedback, in which specific doubts were addressed at all stages. First, a matrix was provided, with all EC identified in a given CS (the number of EC across CS varied from 15 to 89) and all possible ES ($n = 33$). Each CS identified which components (habitat or biotic element) had the potential to sustain or contribute to the supply of a given ecosystem service or abiotic output. Linkages were assigned following a discriminating approach, excluding weak and possibly non-relevant effects of habitats/biotic elements, to avoid reporting trivial linkages which could compromise patterns and identification of relationships. While evaluating the potential of the habitats to support or deliver a given ES/AbO, the role of the associated biological communities (e.g. planktonic, sessile or sedentary species) were also taken into account, even if not explicitly mentioned in the habitat EUNIS category name. The contribution of mobile biotic groups was evaluated separately, by directly associating ES. The identification of links in round one resulted from expert consensus within each case study.

In the second stage, the experts had access to all CS assignments from stage one. When reviewing their previous linkages, a further distinction was made between those habitats or biotic groups with a

relevant but weaker (1) role and those with a very important and stronger (2) role or contribution to sustain a given service (ES or AbO). Zeros were attributed where no links were assigned. The final review and consistency check was conducted in a collaborative exchange process between experts in all CS; where links were checked for relevance.

We used the aggregated information from the seven case study EC-ES linkage matrices in two ways, considering:

- Presence/absence of a link, i.e. non-weighted estimates, acknowledging only the existence (1) or not (0) of a link between an EC and a given ES; and
- Strength of link, i.e. average weight (range between 0 and 2) from an EC to a given ES across all CS reporting that specific EC (i.e. habitat assessment unit).

One CS, LR in Sweden, described its ecosystem components (habitats and mobile biota) but did not report site-specific EC-ES linkages. In this sense, the services supply potential of CS LR habitats were characterized by the mean value of relevant links estimated for those habitats by other CS.

2.4. Statistical analysis

2.4.1. Case studies' variability

The variability in expert valuations was assessed in order to understand the 'strength of evidence' of the baseline data, i.e. consistency. It was measured at the habitat level using the EC-ES links reported by the different CS sharing a given EC (i.e. habitat assessment unit). Consistency was evaluated regarding the link prevalence (i.e. consensus regarding the existence of a specific EC-ES link across CS) and its valuation dispersion (i.e. consensus regarding the magnitude of importance of a specific EC-ES link across CS). For prevalence we considered the number of CS identifying a given EC-ES link among all CS reporting that EC. For dispersion, we used the coefficient of variation (CV), to assess the variability of the experts' grading (0, 1, or 2) across the CS. CV is the ratio of the standard deviation to the mean of weights across CS reporting on a given habitat assessment unit. Because the number of CS reporting a given EC varied, the CV was an appropriate measure allowing for the comparison of groups with different means and sizes.

2.4.2. Ecosystem service supply from habitats and biota

We assessed the overall ES supply heterogeneity across each of the ecosystem components (EC: habitats and biota) independently, using a Sørensen-based multiple-site measure (Baselga, 2010), commonly used in community ecology. The overall heterogeneity depends on patterns of ES co-occurrence involving all the assessment units within the pool for which heterogeneity is measured. For this reason, multiple-site are better than pair-wise dissimilarity measures (Baselga, 2013). Our goal was to compare the patterns of contribution to ES supply between the two types of EC considered in this study: the habitats (and their directly associated biological communities) on the one hand, and the mobile biotic groups on the other. For that we compared the overall multiple-site dissimilarity for habitats' contribution to ES with that of mobile biotic groups. Prior to this analysis, the mobile biotic groups were associated to relevant habitat(s) assessment units (SOM 2 Table S3) and their ES valuations assigned to those habitat categories. Accordingly, the total beta diversity (β SOR), the spatial turnover (β SIM) and the nestedness (β NES) components were assessed for each EC. A pre-transformation of data into presence/absence was performed. The *betapart* R package was used for the calculations (Baselga and Orme, 2012).

In a second analysis, we assessed the dissimilarity of habitats and mobile biota regarding their contributions to ES. For this we used pairwise dissimilarities as computed with the total beta diversity (β Sor, Sørensen index) measure. A dummy variable was added to the

original abundance matrix, with value “1” for all samples, to control for the effect of zero samples (observed in $n = 17$) (Clarke et al., 2006). A Principal Coordinate Analysis (PCO) (Gower, 1966) followed by a Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson, 2001; McArdle and Anderson, 2001) was run to test for significant differences between ES supply patterns from habitats and ES supply accounting only for mobile biotic groups associated with those habitats. The test design consisted of two-factor crossed analysis, with two fixed factors: EC (two levels: habitat $n = 251$; and biota $n = 251$) and CS (seven levels), with n ranging from 11 to 85 habitat units per EC x CS block (in LE and NS, respectively). Type III SS for unbalanced designs was used.

2.4.3. Patterns of ecosystem service supply across aquatic realms and associated ecotones

ES supply contributions from habitats and mobile biotic groups were aggregated to allow a more realistic accountability of a given habitat full potential for services provision. The expert valuation of both habitat and biota ES contributions were summed if assigned to the same habitat assessment unit in a subsequent post-elicitation step (SOM2 Tables S3 and S6). Then the average ES supply by habitat was calculated, as the number of CS reporting under each habitat differs (varying between one and five).

Accordingly, a new resemblance analysis was run for the aggregated ES supply matrix (Bray-Curtis similarity on square root transformed data). Correlations between ES patterns for the newly EC aggregated contributions per habitat assessment unit were extracted (Pearson r coefficient). To test for significant differences in ES supply across realms, a second PERMANOVA was performed on this full similarity matrix (unrestricted permutation of raw data). The test design consisted of one fixed factor ‘Realm’ (12 levels), using Type III SS for unbalanced designs due to unequal number of habitat units per realm. A PCO analysis was performed and the services most strongly correlated with each axis were identified as indicated by the respective strength of the correlations (Pearson r coefficient).

Subsequently, to identify ES bundles, an inverse (r -mode) analysis was run on the variables, i.e. between ecosystem services. Whittaker's Index of Association (IA) was the chosen similarity measure, which takes the value 100 when two ES have exactly the same percentage valuation across the habitat assessment units (full positive association) and in turn the value zero when they are found in completely different habitats (full negative association) (Somerfield and Clarke, 2013). Prior to the analysis, three provisioning related AbO were removed (Non-Renewable Abiotic Energy Sources, Metallic Abiotic Materials, and Nutritional Abiotic Substances Non-Mineral) as they did not occur in any habitat assessment unit, as well as one provisioning ES, Mechanical Energy, due to very low frequency of occurrence (one sample only). Similarity Profiles (SIMPROF) analysis was run to show associations among ES, which covaried consistently across habitat assessment units (Somerfield and Clarke, 2013). SIMPROF allows accounting for the fact that ES are not expected to vary independently of each other. To identify highly associated services a hierarchical agglomerative clustering analysis was run on the previous resemblance matrix, using the Group Average method. The significant groups of ES were finally confirmed by a SIMPROF type 3 test (at a significance level of 2%), using R package *stats* (R Core Team, 2017) to read output resemblance matrix into R, and *clustsig* package to run the simprof tests for checking statistical significance of clusters (Whittaker and Christman, 2014). The ES and AbO valuations of the distinct clusters were plotted together against the habitats ordered according to the PCO ordination axis 1. The distance and permutation based analyses and ordination plots were carried out with the PRIMER v6 & PERMANOVA+ package (Anderson, 2001; Clarke and Gorley, 2006), except where mentioned differently. Finally, a modularity analysis was performed to identify co-occurrence patterns of ES in relation to specific EC. It has the advantage of associating ES bundles to spatial units, by directly identifying meaningful modules of

EC-ES. The similarity in groups of ES that co-occur in the same habitats was assessed for the 30 ES identified in 57 habitat units at EUNIS level 2, in order to summarise patterns at a broader scale. Modularity is a network analysis structural measure for the strength of division into similar modules. Analyses were performed with R package *bipartite* (Dormann et al., 2008, 2009).

2.5. Derivation of an Ecosystem Services Supply score

The weighted EC-ES links compiled from the estimates of the seven CS were the basis for assessing the services supply potential and derivation of an ES supply score (ESS). The ESS is composed by three dimensions (Box 1): 1) the potential to supply; 2) the capacity to supply; and 3) the condition to supply. The ES supply potential refers to the importance of an EC to contribute to an ES, and is assessed based on a qualitative valuation attributed by expert judgement. Secondly, the capacity refers to the actual contribution of the EC to an ES in a given location, and is assessed based on the area occupied, i.e. its representativeness. The rationale being that the greater the area occupied by a given unit (e.g. habitat type) the greater its capacity to provide the ES dependent on that habitat. Thirdly, the condition refers to the actual condition in terms of conservation status or environmental integrity of the EC, in a given location, which is assessed based on the overall habitat condition following the rationale that the more disturbed the environment is, the weaker its capability of providing or supporting an ES.

The ES Supply Condition was characterized based on information available from several EU environmental directives that cover the diversity of ecosystems included here, i.e. aquatic habitats across freshwater to marine environments, and relevant land-water ecotones:

- Favourable conservation status (FCS) of natural habitats and species following the EU Habitats Directive (conservation status classes: Favourable, Unfavourable-inadequate, Unfavourable-bad, Unknown);
- Good ecological status (EQS) of surface waters following the EU Water Framework Directive (WFD) (ecological status classes: High, Good, Moderate, Poor, Bad);
- Good environmental status (GES) of marine waters following the EU Marine Strategy Framework Directive (MSFD) (status classes: Good, Not good).

Although these are different assessment systems, that do not ensure an exact equivalence, they share fundamental similarities that allow merging them for the purpose of this study. First, all three EU Directives assume that status must be assessed as a deviation from some desirable state. Secondly, cross-walks have been established between the EUNIS habitat classification and other hierarchies (<https://eunis.eea.europa.eu>), which facilitate a standardised use of this information in integrated contexts. Moreover, there is a growing agreement that measuring FCS from a carrying capacity point of view is the most adequate approach (Epstein, 2016), which is furthermore in line with the rationale of incorporating this condition dimension into our ESS score. We propose correction factors (Table 2) to be used for incorporating this condition dimension into the ESS score. The distance between classes is not equivalent; instead the penalisation increases initially with distance to the desirable condition, to a point where increasing degradation causes smaller ES provision variation.

For this study, the ESS score was calculated at the habitat assessment units level ($n = 148$). Details of the ESS calculation are provided in SOM 1.

The strength of the correlation between the different dimensions of the ESS score was investigated through Pearson r coefficient.

Box 1

Ecosystem services supply (ESS) score.

The Ecosystem Services Supply score (ESS) has three dimensions: the supply potential; the supply capacity; and the supply condition (Eq. (1)). Prior to aggregation, indicators in dimensions 1 and 2 were normalised using min-max scaling. Each dimension was weighted to reflect its respective conceptual contribution to the characterization of the phenomenon of ecosystem services supply in a given assessment unit. The ESS final score ranges between [0 and 1].

Equation 1:

$$\text{Ecosystem Service Supply score}_a(\text{ESS}) = (n\text{SS}_{\text{Pot}} \cdot 0.5) + (n\text{SS}_{\text{Cap}} \cdot 0.25) + (\text{SS}_{\text{Cond}} \cdot 0.25)$$

where:

a is a given assessment unit

$n\text{SS}_{\text{Pot}}$ is the normalised Services Supply Potential given in Eq. (2)

$n\text{SS}_{\text{Cap}}$ is the normalised Services Supply Capacity given in Eq. (3)

SS_{Cond} is the Services Supply Condition given in Eq. (4)

Dimension 1 | Services Supply Potential
Reflects the importance of an ecosystem component, i.e. habitat assessment unit (which comprises habitat and all its associated communities) for contributing to the provision of ES, and was assessed based on a qualitative valuation (weights: 0, 1, 2) attributed by expert judgement. Valuation was taken individually per each of the 33 ES (at group level) across each habitat assessment unit, by n case studies reporting for a given assessment unit. To deal with varying number of valuations across assessment units (n ranging between 0 and 7), and to express a balanced view of the relative importance of an ecosystem component to a given ES, the arithmetic mean of ES weights across n expert valuations is calculated for each ES in each assessment unit. The supply potential of a given assessment unit is then calculated as the sum of the mean weights of all ES assigned to that assessment unit (Eq. (2)).

Equation 2:

$$\text{Service Supply Potential}_a(\text{SS}_{\text{Pot}}) = \sum_{j=1}^{n_{\text{ES}}} \left(\frac{1}{n} \sum_{i=1}^n W_{\text{ES}i} \right)_j$$

where:

a is a given assessment unit

n is the number of valuations for a given ES in a

i is one ecosystem service valuation

$W_{\text{ES}i}$ is the weight of an ES in a assigned by i

n_{ES} is the total number of ecosystem services in a

j is one ecosystem service

Dimension 2 | Services Supply Capacity

Reflects the actual contribution of the ecosystem component, i.e. its true spatial representativeness, to an ES. The ES Supply Capacity of a given assessment unit is calculated based on the area (km²) occupied by the assessment unit (Eq. (3)).

Equation 3:

$$\text{Service Supply Capacity}_a(\text{SS}_{\text{Cap}}) = \sum_{i=1}^n A_i$$

where:

a is a given assessment unit

n is the number of all spatial patches representing a

i is one patch within a

A_i is the area of each patch in a

Dimension 3 | Services Supply Condition

Reflects the actual condition in terms of conservation status or environmental integrity of the ecosystem component (i.e. assessment unit), which guarantees or, on the contrary, compromises its capability of supplying ES. The ES Supply Condition of a given assessment unit is assessed based on its overall condition according to Table 2 ratings [1, 0.67, 0.25 and 0], and is calculated as the arithmetic mean of the observed conditions (CoS) across all patches (i) comprising an assessment unit (a), weighted by the relative area (A) occupied each patch (Eq. (4)).

Equation 4:

$$\text{Service Supply Condition}_a(\text{SS}_{\text{Cond}}) = \sum_{i=1}^n (\text{CoS}_i * \frac{A_i}{A_a})$$

where

a is a given assessment unit

n is the number of all spatial patches representing a

i is one patch within a

A_i is the area of each patch in a

A_a is the total area of a

CoS_i is the conservation status of each patch in a

Table 2

Correspondence of status classes across three condition assessment schemes from the EU Directives (Habitats, Water and Marine Strategy) and respective correction factors for calculating Conservation Status (CoS) Service Supply Condition parameter in dimension 3 of the ES Supply score in Box 1. FCS: Favourable Conservation Status; EQS: Ecological Quality Status; GES: Good Environmental Status.

Status classes correspondence			Correction factor	Normative definition
FCS (habitats and species)	EQS WFD	GES MSFD		
Favourable	High		1	The potential and capacity to produce ES is not altered
	Good	Good		
Unfavourable-inadequate	Moderate	Not good	0.67	The potential and capacity to produce ES is decreased by a third
	Poor			
Unfavourable-bad	Bad	–	0.25	The potential and capacity to produce ES is decreased by 3/4
			0	Total loss of ES supply

3. Results

3.1. Case studies' variability

As expected, with larger areas the chance of encountering a higher number of unique habitats increased (Fig. 2) (Pearson $r = 0.89$ of logarithmic regression, $n = 8$). This strongly influenced the number of links to ecosystem services that are identified in such areas, which also tended to increase (Pearson $r = 0.90$ of linear regression, $n = 7$). However, the number of links to services were found to be even more strongly related with the number of unique habitats within a case study (Pearson $r = 0.99$ of logarithmic regression, $n = 7$). Despite that the size of the CS and the diversity of EC encountered within an area contribute positively to the local services supply; we observed decelerating patterns in the increasing trends of the number of unique habitats with area (Fig. 2) and of the number of services links with unique habitats (SOM1 Fig. S1).

There was great consistency among CS regarding the role of an EC for services provisioning. In widespread ECs ($n = 71$), the CS consistently evaluated 71.2% of the cases, i.e. EC-ES pairs. This means that consistency occurred both when identifying the relevance of the habitat for a given ES supply (13.6% of the cases, corresponding to 318 identified links, independently of the valuation attributed to the link), and when refuting the contribution of a given habitat for a given service (57.6% of the cases, corresponding to 1350 absences of a link). Only 28.8% of the cases did not reach the consensus of all CS sharing an EC. Still, within these, for 81% of the links at least half of the case studies agreed on the EC-ES link valuation (0, 1, or 2). The low agreement cases, i.e. where less than half of the case studies concurred on the valuations, represented only 2.6% of the total number of links in the data. However, approximately half of the habitat units ($n = 78$) were reported by a single case study, thus those links are based on unique estimates.

The variability in the valuations of an EC-ES link, i.e. the relevance of an EC to provide or support services, was calculated for those EC occurring in more than one CS ($n = 71$). The mean coefficient of variability across habitats was 0.82; although habitats in 'Other' realms showed larger dispersion regarding ES valuation (mean CV = 1.49) than habitats in aquatic realms (mean CV = 0.81; SOM 1 Table S7). It was also observed that the variability among the expert valuations was higher regarding the role of habitats towards abiotic outputs of the system (mean CV = 1.22) than for biologically mediated services (mean CV = 0.74). The highest variability was found for 'Nutritional Abiotic Substances Mineral' (mean CV = 1.58) and 'Water' (mean CV = 1.40), while the highest agreement between expert valuation across all habitats was found for biologically mediated 'Intellectual Representative Interactions' (mean CV = 0.25) and 'Pest & Disease Control' (mean CV = 0.25). Overall, the mean CV across services valuation was 0.92.

3.2. Heterogeneity in ecosystem service supply from ecosystem components

Multiple-site dissimilarities revealed that the estimated overall beta diversity in relation to ES provision was very similar for habitats ($\beta\text{SOR} = 0.98$) and mobile biota associated to those habitats ($\beta\text{SOR} = 0.97$), with a higher turnover of ES across habitat units for habitats ES contribution than for that of the mobile biota ($\beta\text{SIM}_{\text{hab}} = 0.94$; $\beta\text{SIM}_{\text{bio}} = 0.69$). This indicates that a higher spatial heterogeneity of ES provision is observed within habitats than within the mobile biota. Very little nestedness effects ($\beta\text{NES}_{\text{hab}} = 0.04$; $\beta\text{NES}_{\text{bio}} = 0.09$) were observed, meaning that the heterogeneity of ES is almost completely caused by ES replacement within each group (habitat or biota), indicating a high complementarity between habitat units regarding the supply of ecosystem services.

When compared, the ES supply spatial patterns differed whether habitats or just mobile biotic groups contributions were considered

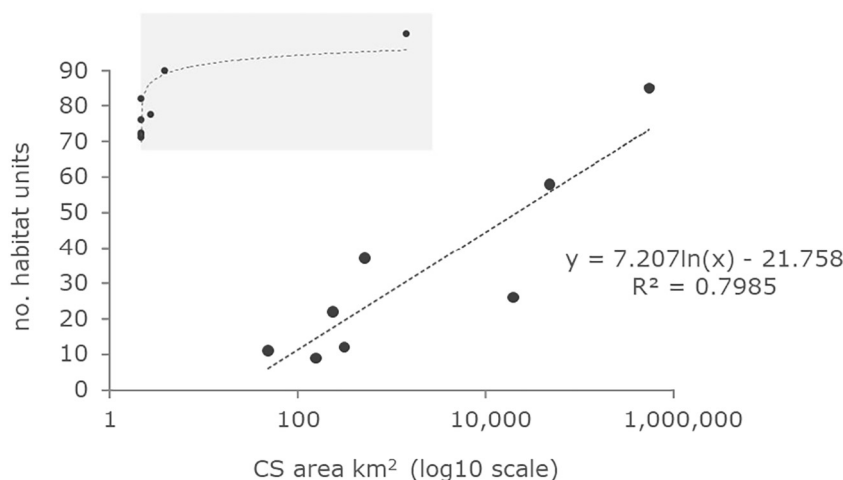


Fig. 2. Linear-log plot of the number of habitat units reported in relation to the area (log10 scale on untransformed data) in the eight case studies. Top left plot presents data trends on normal scale. Logarithmic regression equation describing both plotted trend lines indicated.

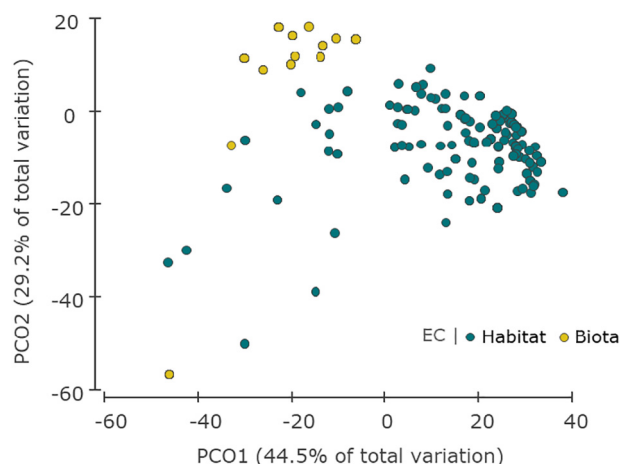


Fig. 3. Ordination plot derived from Principal Coordinates Analysis (PCO) based on the Sørensen similarity on ES supply by the ecosystem components (EC) habitats and by mobile biotic groups for the same habitat units.

(Fig. 3, Table 3). Such differences were consistent across all CS, with all pairwise tests indicating significantly lower average similarity ($p < 0.001$) between levels of factor EC: habitat and biota, than within (SOM 1). The maximum observed similarity across EC levels was 57% (range [33–57%] across CS), just below the minimum observed similarity within habitat or biota levels (range_{hab} [59–85%] and range_{bio} [58–100%] across CS). The PCO showed that similarity within ES supply provided by biota across the different habitats units was in average higher, with most of the samples lumped together in the ordination plot, despite the same number of samples for biota and habitats ($n = 251$ each). This is in line with the higher spatial turnover observed for habitat services than for mobile biota services.

The habitats with highest mean ES supply potential tended to present also the highest ES supply from the mobile biotic groups associated to them (Pearson $r = 0.60$, $n = 149$; Fig. 4), despite that, ES supply valuation for mobile biota was conducted independently from their habitats' filiation. Nevertheless, highly mobile biotic groups contribute with less ecosystem services (11 ES types in total) than the habitats themselves with their closely associated communities.

The mobile biotic groups that depend on aquatic environments contribute essentially to cultural services, followed by an important role for regulation services, namely pest or disease control, waste mediation, atmospheric composition and climate regulation, and life cycle maintenance, habitat, and gene pool protection (Fig. 5). Finally, a relevant contribution to provisioning services related with biomass for nutrition was identified; to a lesser extent biomass as material, was also attributed to them. Logically, no pure AbO was related to the biotic groups. Comparing the services supplied by mobile taxa with the ES to which habitats contribute the most (Fig. 5), it was observed that the ES ranking higher in habitats are also provided by the biota, namely physical and intellectual cultural services and the regulating services lifecycle maintenance and waste mediation by biota. However, some of the services strongly associated to mobile biota, such as pest and disease control,

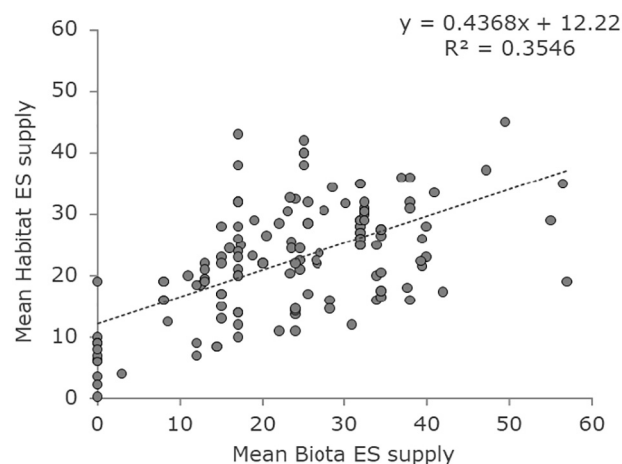


Fig. 4. Relationship between overall mean ES supply from habitats and from mobile biotic groups across all unique habitats units reported in this study.

biomass for nutrition, or spiritual values, do not rank high in habitats contribution to ES.

In addition, there were 14 habitats belonging to non-aquatic realms in other domains ('Terrestrial Natural' ecosystems, 'Agricultural' and 'Urban' areas) which do not support aquatic dependent fauna, and thus services associated to those biotic groups were not provided by these habitat units.

3.3. Patterns of ES supply across aquatic realms and associated ecotones

Once the habitat and mobile biotic ES contributions were aggregated according to the habitat units in which they co-occurred, all aquatic EC revealed a potential to provide at least seven different types of ES or AbO. This excluded the EC in 'Other' non-targeted realms, i.e. terrestrial natural habitats, agricultural, and urban, to which a lower number of services was often associated. Non-renewable abiotic energy sources, metallic and non-mineral abiotic outputs of the system were the only three non-biologically mediated services that have not been reported as relevant outputs from aquatic or related ecosystems, by any of the CS.

There are important differences across aquatic realms regarding the number of habitat units within each category (Fig. 6). Coastal waters are the most diversified realm with 32 different habitat units, while the 'Urban' realm is the least diverse, including only three different habitat types. Those differences are partially related with the resolution used to characterize habitats. Aquatic realms were almost exclusively reported at EUNIS level 3, with 71 to 92% of their habitat units described at this resolution. Realms in 'Other' domains and the FW 'Riparian' realm were commonly reported at EUNIS level 2 (rarely EUNIS 1), with at most 50% of their habitat units described at the more detailed resolution used in this study (EUNIS 3).

Ecosystem services supply varies significantly across all aquatic realms and associated non-aquatic environments, except between 'Lakes' and 'Rivers' (Table 4). Lakes and rivers presented 86% similarity in ES supply patterns, the highest across realms similarity observed. The average similarity between realms was higher for realms within a same domain (81% for Marine, 79% for Coastal, 77% for Freshwaters) than for realms across domains (64% for Marine vs all other; 61% for Coastal vs all other; 59% for Freshwaters vs all other). As expected the 'Other' non-targeted realms in non-aquatic environments ('Agricultural', 'Terrestrial Natural' and 'Urban') presented fewer similarities in ES supply with the remaining realms (average similarity of 34%) but even lower between them (average of 27% similarity ranging between [17–41%]) (Fig. 7). Urban settlements were the most different, presenting only an 18% (std dev = 2.53%) average similarity to the remaining eleven realms considered in this study.

Table 3

PERMANOVA results based on Sørensen index similarity for ES supply patterns between ecosystem components (EC) considering Case Studies' assessments (CS) in a two-way crossed design.

Source	df	SS	MS	Pseudo-F	P (perm)	Unique perms
EC	1	1.1218E5	1.1218E5	197.21	0.001	999
Case study	6	81316	13553	23.825	0.001	998
EC × CS	6	44949	7491.5	13.169	0.001	998
Residuals	488	2.776E5	568.85			
Total	501	5.9189E5				

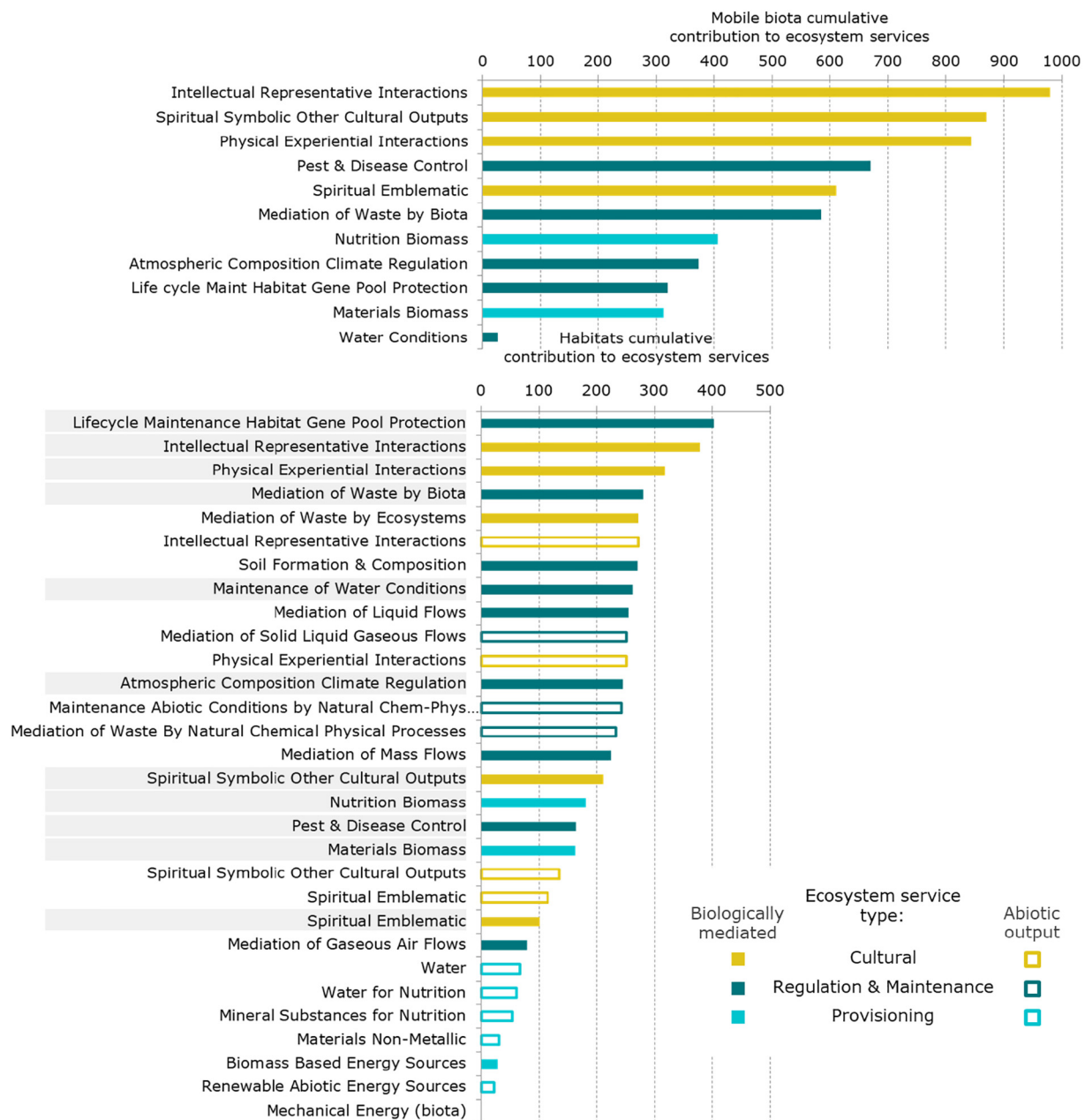


Fig. 5. Bundles of services provided or most associated with mobile taxa versus the services provided by habitats without the mobile biota.

The first two axis of the PCO explained only 51.85% of the variation found among the habitat assessment units regarding services supply (Fig. 7). Biologically mediated ES contributed more than AbO to explain the variation observed in the biplot (Fig. 7). The majority of the ES presented a positive correlation with PCO1 (Table 5), indicating that habitats within targeted realms, i.e. those in marine, coastal and freshwater domains, are positively correlated with these ES. The biologically mediated ES appear more strongly correlated with axis one than AbO (Table 5). Only three AbO appear moderately and positively correlated with PCO1 (>0.40), which are the 'mediation of flows (solid, liquid, gaseous flows)' and the 'physical experiential interactions' and 'intellectual representative interactions'. Variation along the second axis was better explained by three cultural abiotic outputs of the system negatively correlated with PCO2 (Table 5), namely two outputs regarding 'physical and intellectual interactions', and the 'spiritual symbolic and other interactions with land seascapes physical settings' ('spiritual emblematic'). These were associated with urbanized areas (Fig. 7), indicating a possible shift of cultural services and outputs of the system with increasing human

occupation (Fig. 8). Also moderately, but positively, correlated with PCO2 was the biologically mediated service on regulation and maintenance through 'mediation of gaseous air flows'. This service was associated with, for example, riparian woodlands in several case studies (IBRM, DRB, LE, RAV, SwP).

Ecosystems services variation across the different realms showed (Fig. 8), for example, that some ES or AbO were well supported by all aquatic realms and related ecotones, while others, such as different types of provisioning services, were only supplied by some realms (Fig. 8). However, although the average potential for providing some services may be similar for habitats in different realms, when we assessed the realm full potential, its cumulative contribution, the patterns were quite distinct. In some realms the habitat richness and heterogeneity had a boost effect on the potential to supply ES.

Several ecosystem services (both ES and AbO) were highly correlated with each other (Pearson $r > 0.75$), when analysing the habitat assessment units from the samples perspective (Q-mode type analysis). This was the case for some abiotic outputs of the system above

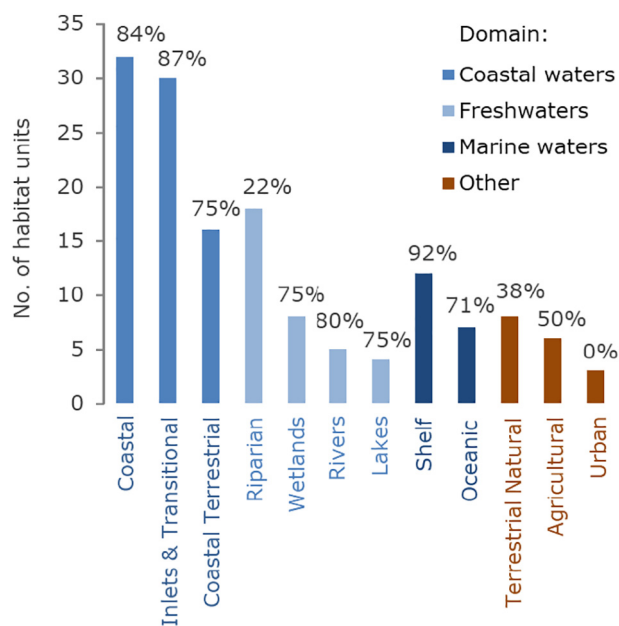


Fig. 6. Number of habitat units reported per realm across the four main domains covered by the 12 realms, with indication of the percentage of habitat units in each realm that are described at the highest resolution level used in this study (EUNIS 3).

mentioned (R&M 'Mediation of Flows (Solid, Liquid, Gaseous Flows)' and 'Cultural Physical and Intellectual Interactions'), but also for provisioning related abiotic outputs of the system such as 'water' either as 'abiotic material' or as 'abiotic nutritional substance'. The biologically mediated ES most highly correlated were: R&M services 'Mediation of waste and Maintenance of Physico-Chemical Biological Conditions', in particular 'Life-cycle Maintenance Habitat Gene Pool Protection'; cultural services ('Intellectual Representative Interactions with Spiritual symbolic and other interactions with biota ecosystems and land seascapes environmental settings', both 'Spiritual Emblematic' and 'Other Cultural Outputs'), and the cultural ES 'Physical and Intellectual Interactions and Spiritual symbolic and other interactions' with the R&M ES 'Maintenance of Physico-Chemical Biological Conditions Pest Disease Control'. However, there were also many services negatively correlated with each other, although mostly showing low strength correlations ($r < 0.4$).

In fact, when evaluating how ES (variables) vary in relation to each other across habitats, we found that some ES are more associated than would be expected by chance, as indicated by the highly significant Type 2 SIMPROF tests for ES across the habitat assessment units ($\pi = 0.063$, $p < 0.001$). An excess of negative associations was observed in the profile (real profile below the lower 99% limit) (SOM 1 Fig. S2), reflecting a high ES turnover across the spatial assessment units (habitats).

There were five significantly different groups of services, according to the SIMPROF type 3 test ($p \leq 0.029$), whose group patterns of distribution across habitats are closely associated with each other (Fig. 9).

Abiotic provisioning services presented clearly distinct patterns from services in the other groups. One group contained the 'renewable abiotic energy sources' and 'non-metallic materials' (Group 1), another 'nutritional mineral substances' and 'water' (for nutrition or as material) (Group 3). Also, 'biomass based energy sources' and biologically mediated 'gaseous flows' (Group 2) formed a distinct group of services regarding their occurrence patterns, while the 'spiritual and emblematic' cultural abiotic outputs (Group 4) appeared isolated from the rest of services. A fifth larger group contained all the remaining biologically mediated ES and AbO, indicating that the majority of the services showed similar patterns of occurrence across habitats.

To identify the co-varying patterns of the different groups of services, the distribution of the ES valuations in each group, i.e. the coherent curves (SOM1 Fig. S3), were plotted against the habitat assessment units ordered according to the first PCO axis, which explain approximately 37% of the variability found across the habitats (Fig. 7). Despite PCO first axis was used, the services in groups 2 and 4 showed a higher strength of association with the second axis of the PCO, as indicated by the ES and AbO correlations in Table 5. This pattern underlines that services in Group 5 are those most strongly supplied by the habitat types considered in this study, i.e. that present a higher mean valuation across habitats (Fig. 8).

When analysing further the co-occurrence of ES in relation to the main habitat types, we found four main groups (Fig. 10), identified at a coarser level (57 habitats at EUNIS 2). Marine and coastal waters habitats emerged more related with cultural abiotic outputs; provisioning of biologically nutritional substances and of both biotic and abiotic materials; abiotic mediation of flows and climate regulation; and waste mediation by biota (Group D). The pelagic water column habitats in marine to coastal waters emerged however grouped with running and standing freshwater habitats, as habitats associated with the co-occurrence of energy and water provisioning, cultural services related with both physical and intellectual or symbolic representations; and also, with regulating services related with lifecycle maintenance and gene pool protection and pest and disease control (Group A). Group A of services co-occurred in a more heterogeneous type of habitats, covering almost all realms studied. Group B services were essentially regulating services, biologically mediated or not, on mediation of flows and waste, regulation of soil formation and water conditions, and maintenance of physical-chemical conditions. Biomass energy provisioning was also included in this group of services that co-occur in estuarine habitats, riparian areas and terrestrial natural environments (in the vicinity of but non-dependent on aquatic systems). Finally, a smaller module (Group C) of abiotic outputs such as water and mineral substances and also spiritual and emblematic services co-occurred in shelf marine waters and urbanized areas.

3.4. Ecosystem Services Supply score

The highest ESS score was obtained in habitat pelagic water column in shelf marine waters, while the lowest in urbanized areas, in particular in constructed, industrial and other artificial habitats. In general,

Table 4
PERMANOVA results based on Bray-Curtis similarity for ES supply patterns across realms (12 levels), showing pairwise tests only for non-significantly different levels within main term 'Realm'.

Source	df	SS	MS	Pseudo-F	P (perm)	Unique perms
Realm	11	54470	4951.8	14.605	0.001	997
Residuals	137	46451	339.06			
Total	148	1.0092E5				
Pairwise comparisons (only non-significant tests shown)						
Groups	t-Test		P (perm)		Unique perms	
Lakes, Rivers	0.78457		0.612		126	

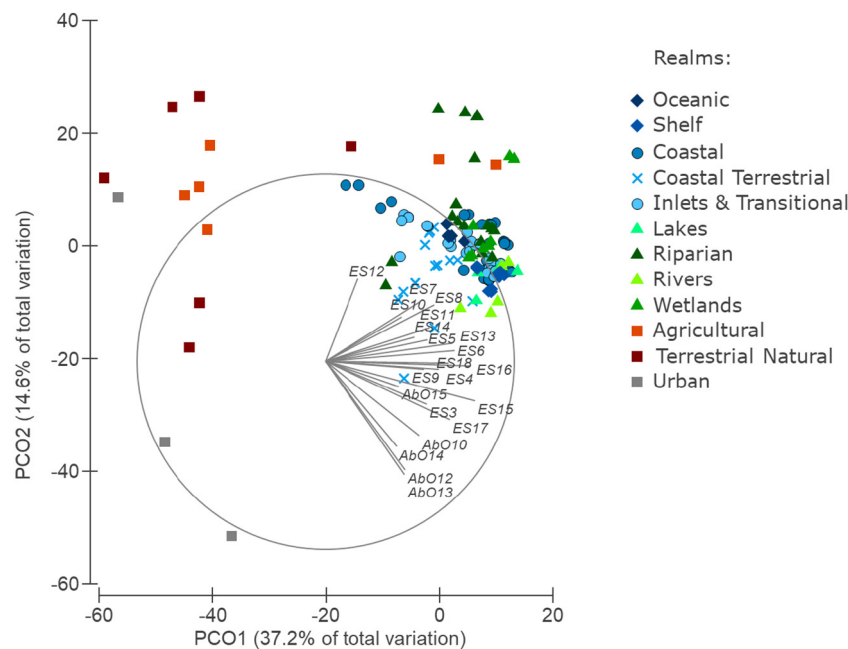


Fig. 7. Principal coordinates analysis (PCO) biplot based on the Bray-Curtis similarity of ES supply across realms (on square root transformed data). ES correlated with PCO axes are plotted (if $r > 0.4$).

habitats in other non-aquatic realms had lower ESS scores than all other habitats (Fig. 11).

The three dimensions that compose the ESS score were not strongly correlated with each other (SSPot vs. SSCap $r = 0.25$; SSPot vs. SSCond $r = 0.31$; SSCap vs. SSCond $r = 0.41$) confirming that they were complementary measures that contributed with substantially different information to the score. Instead, each dimension correlated relatively strong with the final ESS score (Fig. 11), which indicates that no dimension alone was forcing the ESS score result by itself.

4. Discussion and conclusions

4.1. Ecosystem components contribution to ecosystem service supply

It is important to understand size effects (Gotelli and Colwell, 2001) in ES supply well, because of the implications for ecosystem based

management. While our study found positive effects of area size and habitat richness for services supply, it indicates also a saturation point for both habitats' richness and links to services with area. However, it does not allow further insights on whether or at which point a continuous increase in the number of habitat units in relation to area of those units could ultimately reflect high habitat fragmentation rates and, consequently, a negative effect on services supply would be noticeable. Contradictory evidences towards the signal of this size-ES supply relationship seem to be dependent on the ES valuation method, the type of service considered, and even the socio-ecological context, for example population density (Brander et al., 2006; Reynaud and Lanzaova, 2017). Nonetheless, for some ecosystems services in wetlands (Brander et al., 2006) and lakes (Reynaud and Lanzaova, 2017) there were no evidences that the economic value of the services was influenced by the size (area), while for other services negative trends have been identified, i.e. decreased return with area. Testing with a wider

Table 5

Pearson correlations (r) of services (ES and ABo) with the first and second axes of the PCO in Fig. 7. Coefficient values $r \geq 0.45$ in bold. C – Cultural; P – Provisioning; RM – Regulation and Maintenance. Services ordered by decreasing correlation strength with PCO1. Services' full name is provided as Supplemental online material (SOM 1 Table S4).

Service short description	PCO1	PCO2	Service short description	PCO1	PCO2
ES15 C PhysIntel PhysicalExperientialInteractions	0.792	−0.208	ES10 RM MedFlo MassFlows	0.404	0.240
ES16 C PhysIntel IntellectualRepresentativeInteractions	0.771	−0.023	AbO15 C SpiritSymb OtherCulturalOutputs	0.388	−0.134
ES6 RM MaintPhChBioCond PestDiseaseControl	0.683	0.058	AbO14 C SpiritSymb SpiritualEmblematic	0.379	−0.453
ES13 RM MedWast MediationBiota	0.673	0.098	AbO9 RM MaintPhChAbioCond	0.308	−0.242
			ByNaturalChemicalPhysicalProcesses		
ES17 C SpiritSymb SpiritualEmblematic	0.658	−0.309	AbO6 P NutAbSubst Water	0.233	−0.189
ES18 C SpiritSymb OtherCulturalOutputs	0.653	−0.008	AbO3 P AbMat Water	0.219	−0.171
ES4 P Nut Biomass	0.601	−0.040	AbO11 RM MedWast ByNaturalChemicalPhysicalProcesses	0.201	−0.136
ES8 RM MaintPhChBioCond WaterConditions	0.576	0.302	AbO7 P NutAbSubst Mineral	0.197	−0.232
ES11 RM MedFlo LiquidFlows	0.553	0.182	ES12 RM MedFlo GaseousAirFlows	0.171	0.440
ES5 RM MaintPhChBioCond	0.539	0.115	AbO1 P EnAb RenewableAbioticEnergySources	0.146	−0.098
LifecycleMaintHabitatGenePoolProtection					
ES3 P Mat Biomass	0.538	−0.228	AbO5 P AbMat NonMetallic	0.077	0.015
ES9 RM MaintPhChBioCond	0.524	−0.040	ES2 P En MechanicalEnergy	0.052	0.120
AtmosphericCompositionClimateRegulation					
ES7 RM MaintPhChBioCond SoilFormationComposition	0.499	0.314	AbO2 P EnAb NonRenewableAbioticEnergySources	–	–
AbO10 RM MedFlo BySolidLiquidGaseousFlows	0.497	−0.396	AbO4 P AbMat Metallic	–	–
ES14 RM MedWast MediationEcosystems	0.474	0.131	AbO8 P NutAbSubst NonMineral	–	–
AbO12 C PhysIntel PhysicalExperientialInteractions	0.424	−0.578	ES1 P En BiomassBasedEnergySources	−0.136	0.253
AbO13 C PhysIntel IntellectualRepresentativeInteractions	0.421	−0.605			

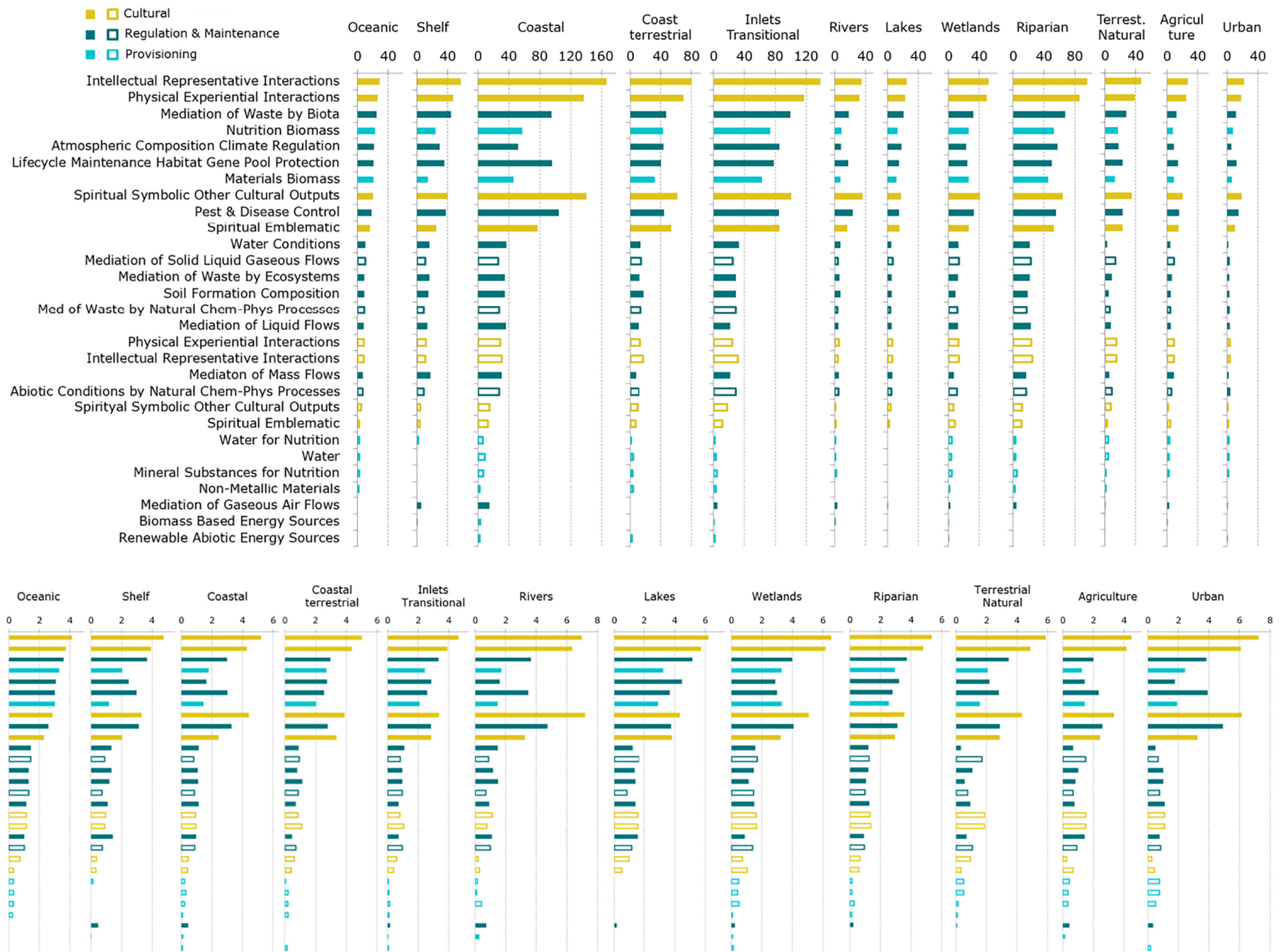


Fig. 8. Distribution of ecosystem services (filled bars) and abiotic outputs of the system (empty bars) across the 12 realms included in this study. Magnitude of expression refers to the cumulative valuation of all habitats (including mobile biota) within a realm for a given service, for the top graphs, and the mean average value of habitats within a realm for the provision of services, for the bottom graphs. Services are ordered by decreasing contribution of a realm to it, starting with oceanic realm and sequentially.

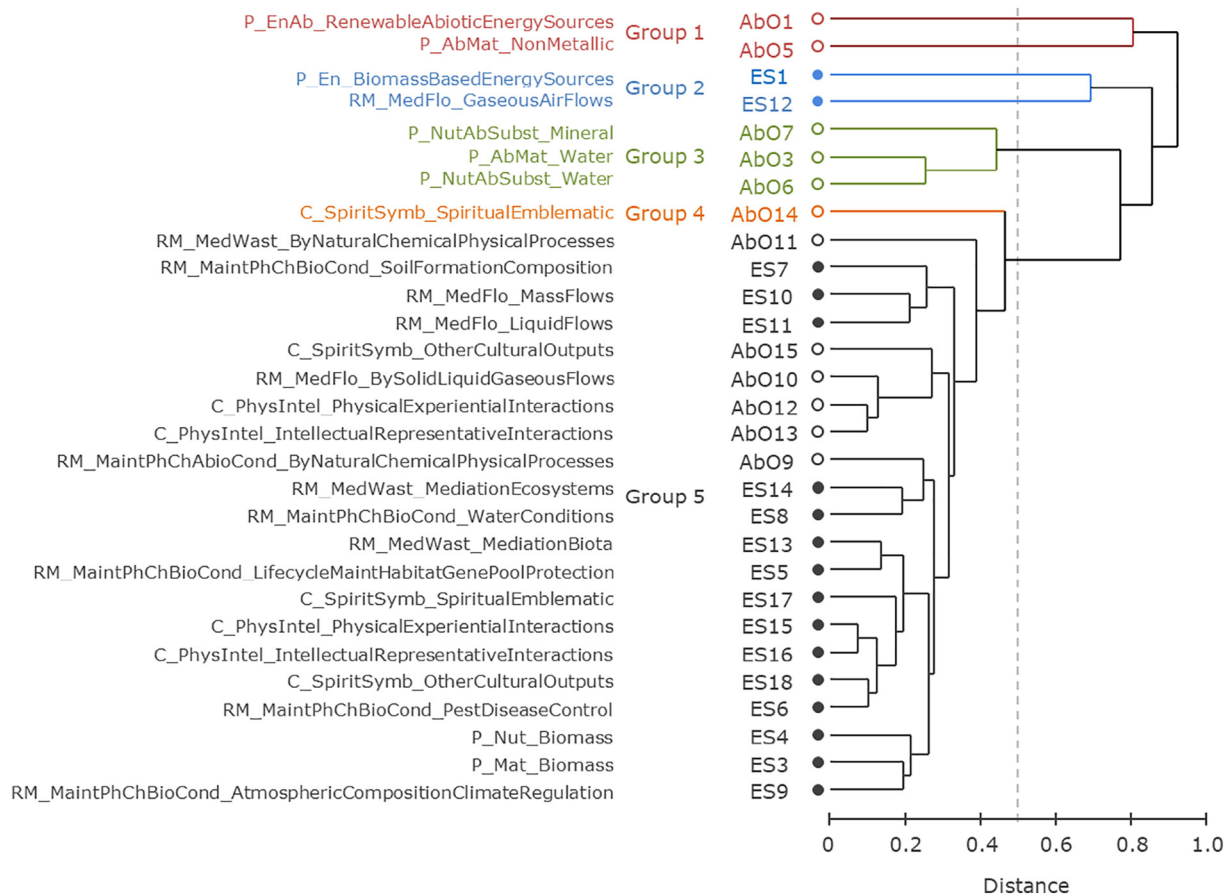


Fig. 9. Dendrogram from (r-mode) group-average clustering of the most relevant 29 services, based on Whittaker's Index of Association among ecosystem services (ES) and abiotic outputs of the system (AbO). Five significantly different groups could be distinguished ($p < 0.02$). Dashed vertical line indicates distance of 0.5. P – Provisioning; RM – Regulation and Maintenance; C – Cultural.

range and more balanced representation of different size areas, coupled with critical explanatory variables, would help to understand if the richness saturation curves, as recognized for species (Gotelli and Colwell, 2001) can be, also observed for ecosystem service(s) and in which circumstances.

Our results make the case for additional protection of habitats that support certain biotic groups during stage(s) of their life cycles, and indirectly contribute to the services specifically provided by such groups. This is supported by the complementarity found in the services supplied by mobile biotic groups, which are not associated to a single habitat and, thus, the importance of considering their ES when assessing the supply potential of those habitat units. This will reflect more accurately the intrinsic value of a habitat for services supply in two ways. First, it represents an added contribution to the shared services already secured by that spatial unit. Secondly, it takes into account new bundles of ES, such as pest and disease control, biomass for nutrition, or spiritual values, which emerged more strongly associated with mobile biota.

4.2. Patterns between ecosystem services and across aquatic realms

Evidence for high turnover of ES across different habitats was found, while services with strong co-occurring patterns were associated in bundles (Figs. 9 and 10), sensu Raudsepp-Hearne et al. (2010). These evidences point to differences in ES spatial patterns across aquatic ecosystems and associated ecotones, as revealed by the significant differences found across all realms, except for 'Lakes' and 'Rivers'. These two freshwater realms emerge in fact linked to the same bundle of ES (Fig. 10), with a strong prevalence of cultural and regulation and maintenance services, as also described for lakes worldwide (Reynaud and

Lanzanova, 2017). Our findings contradict previous evidence gathered across marine and freshwater habitats (Boulton et al., 2016) and point to significant differences regarding their ecosystem services' supply spatial patterns. While Boulton et al. (2016) found no evidence for considering different services when dealing with conservation issues in marine and freshwater habitats, our results showed that not only across those realms, but even within realms, there are significant differences regarding ES supply. Because several bundles of ES for different habitats were revealed by the modularity analysis (Fig. 10), such spatial differences and complementarity need to be considered in conservation management. The loss of specific habitats may lead to the loss of multiple related services provided by a specific aquatic system. This spatial heterogeneity in services supply is even more relevant if we consider that different ecosystem components are under different impact risk levels (Borgwardt et al., 2019), due to human activities usually targeting the exploration of specific services (Culhane et al., this issue). Effective EBM needs to consider, in addition, that there is often a spatial separation of activity location and pressure effect and that non-target habitats and their associated services supply may still be negatively impacted. Acknowledging spatial differences in ES distribution patterns across aquatic ecosystems will support a better spatial planning (O'Higgins et al., 2019).

Evidence from literature highlights instead the important role of ecological connectivity within and among different habitats (Boulton et al., 2016). Although not addressing connectivity directly, our study included a wide continuum across twelve realms. The results indeed point at the importance of accounting for flows between aquatic-terrestrial ecotones. These transitional environments are not only important contributors of complementary ES and AbO, but they also



Fig. 10. Groups of ecosystem services (columns) that co-occur in the same habitats (rows), for the 30 ES identified in 57 habitats at EUNIS 2, according to modularity analysis. Realm and Domain to which each habitat unit belongs is indicated.

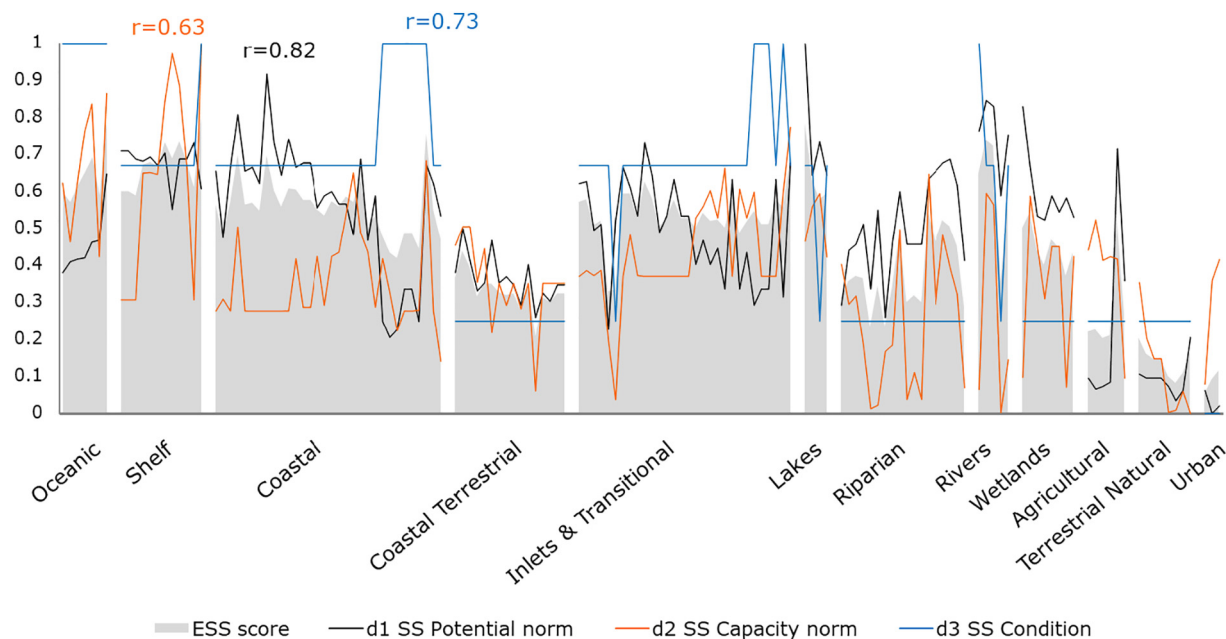


Fig. 11. Ecosystem Services Supply score (ESS) variation across the 148 habitats in different realms. The three dimensions that compose the ESS score are plotted as lines in the graph along with the Pearson r coefficient of each dimension and the total score.

promote many of the ES delivered by the associated realms. Riparian habitats, for example, deliver mainly regulation and maintenance services as revealed by the modularity analysis (Fig. 10). These services are necessary to keep the integrity of the aquatic ecosystem (e.g. by maintenance of water conditions, flood protection, stream bank stabilization) (Vigiak et al., 2016) and to promote the ES provided by rivers and lakes (e.g. water for nutrition or irrigation, recreational aquatic sports). However, biodiversity and ecosystem integrity in these transitional habitats, such as riparian, wetlands, or coastal dunes, are in turn highly dependent and affected by dynamic hydrologic inputs from strictly aquatic EC (Acreman et al., 2000; Vigiak et al., 2016). ES supply depends on the equilibrium of these relationships to ensure the provisioning of related services.

The identification of these links is crucial for targeting integrated management actions across spatial units and habitat types. Urban, agricultural and forest production land claim are some of the threats to the riparian systems (Weissteiner et al., 2016; Borgwardt et al., 2019). The ESS score showed that the diminished ecological condition in riparian habitats is compromising their potential to provide such services (Fig. 11). Also, semi-natural urbanized areas and agricultural fields do not contribute with the same type of services as riparian natural habitats, with their overall ESS potential being lower (Figs. 8 and 11). A similar trend is observed when riparian natural habitats are replaced by other natural habitats (e.g. those from the terrestrial natural realm). Although these realms share the same ES bundles (Fig. 10), their ES supply potential is overall lower than that of natural riparian habitats, representing a net loss of ecosystem services.

This linkage framework provided a comprehensive approach accounting for all potential aquatic dependent ES from freshwater to marine environments, and can be applied to new cases for unravelling potential relevant linkages in these systems based on the patterns identified here.

Although not addressed in this study, a thorough analysis of the potential ES trade-offs and synergies can be supported by our approach within specific CS contexts. Several studies have addressed this issue (Boulton et al., 2016; Lee and Lautenbach, 2016; Rodríguez et al., 2006) but acknowledge that, due to the influence of the socioeconomic drive, trade-offs are better predicted when the demand-side of ES and AbO is taken into account within spatial and temporal specific

scenarios (Crouzat et al., 2016). Our expert based assessment approach provides a potential for ES supply, irrespective of the actual status of the ecosystem components. However, the extent at which the actual conservation status may influence the perception of service provision (Mouchet et al., 2017) may also influence experts' valuation about relevant biodiversity links to ecosystem services.

Several studies found sufficient evidence that biodiversity influences certain provisioning and regulating services the most (Cardinale et al., 2012). Our results for aquatic and related habitats support that these services are the most affected by the effects of anthropogenic impairments. The ES patterns, where anthropogenic land-use change has occurred, showed a decrease in the supply potential of those services (Figs. 7 and 8). The cultural services, however, seem to persist comparatively well represented in these 'Other' realms; in particular, 'physical and experiential interactions' (e.g. aquatic sports like surf or canoeing) and 'intellectual and representative interactions' (e.g. scientific, heritage; entertainment). Near water environments, in the coast or inland, are traditionally leisure and recreational places and one would expect that naturalness would be an indubitable requirement for cultural services potential (Hermes et al., 2018). However, our study seems to indicate that it is not necessarily the case. The value attributed to certain landscapes for cultural, especially recreational, services may consider other aspects than naturalness, such as conditions to sports practice, infrastructure and ease of access. These facilities supporting outdoors activities may jeopardize provisioning or regulating services while promoting cultural ones.

Some of the provisioning AbO showed patterns restricted to specific habitats (Fig. 9), in particular 'renewable abiotic energy sources', 'non-metallic materials' as well as 'nutritional mineral substances' and 'water' (for nutrition or as material). It is rather unexpected, given this study focuses on aquatic systems, such a low valuation of aquatic habitats to provide services such as energy from hydropower or waves energy, and water for nutrition or other uses such as irrigation, industrial and domestic use. The CS assessments might have been conditioned by the experts' local perceptions about the uses in place regarding the exploitation of energy sources, or about the condition of the system, for example water pollution compromising drinking water uses. This demonstrates the inherent difficulty, when evaluating ecosystem services, of distinguishing clear supply of services from demand; and potential to supply from condition to supply.

Three services have not been linked to any habitat in this study. The 'non-renewable abiotic energy sources' were considered not applicable to aquatic systems, considering the examples provided in CICES - coal, oil, gas. These are not a direct output of aquatic systems, or the habitats under which they occur, but originate from deeper soil layers outside the range of our habitats types. In addition, they have also been generated at completely different time scales, which makes it even more difficult to attribute them to the habitat units in the spatial and temporal context of the current assessment. In this sense, they were not considered in this study for the purpose of assessing EC-ES linkages in aquatic ecosystems. However, their exploitation may occur in places where it causes a disturbance in aquatic environments (e.g. oil and gas platforms standing in the seabed habitats) and in those cases they should be considered instead as human activities and pressures in the affected habitats (see Borgwardt et al., 2019). As for the 'metallic and non-mineral' abiotic outputs of the system, these resources either are non-existent or not exploited in the CS areas and, thus, not an obvious service of aquatic and related ecosystems.

Finally, when considering the biologically mediated services and the AbO of the system, which are considered with a similar structure in the classification used in this work (SOM 1 Table S4), there is evidence that services of the same 'Group' (considering CICES levels) seldom co-occur in the same realms or habitats (Fig. 10). This may suggest that in order to secure the provision of a comprehensive portion of ES, it is purposeful to preserve a high diversity of realms or habitats.

4.3. Ecosystem Services Supply score

The ecosystem services supply (ESS) score presented here allows comparing current services supply across aquatic systems in Europe (Fig. 11). Strictly aquatic habitats from marine to freshwaters (six realms in oceanic, shelf, coastal, inlets and transitional waters, lakes, and rivers) present an overall higher ESS score (mean ESS = 0.61) than non-aquatic associated realms (mean ESS = 0.39) and habitats in other realms (mean ESS = 0.17). This is partially due to the worst ecological condition (SS_{cond}) verified for the coastal terrestrial ecotones, riparian and wetlands, which are habitats under multiple pressures (Borgwardt et al., 2019). In fact, they are among the most threatened habitats in Europe according to the recent EU Red List of Habitats (EEA, 2017). In a scenario where the environmental targets for these habitats are achieved, under the different policies regulating their conservation status (e.g. WFD, MSFD, Nature Directives, Nitrates and UWWT Directives), there is a probability of a 26–47% increase in these habitats' ESS. This improvement does not even consider any change in relation to the supply capacity (SS_{cap}) in terms of area gained, for example due to measures for recovering habitats' lost area. The BES relationships seem to differ among ES and to depend on approaches to link them, for example spatially, management linkage, and functional linkage (Ricketts et al., 2016). The ESS score can complement an integrative and comprehensive linkage framework, that links demand and supply sides, and contribute to elucidate, if improvements on the environmental condition component (SS_{cond}) result in either positive or negative changes in particular services. This information can provide a better understanding of biodiversity dependencies patterns in particular to ES/AbO, and also of potential trade-offs and synergies, between ES/AbO (Lee and Lautenbach, 2016).

The Services Supply Potential (Dimension 1 of the ESS score) is particularly important for providing a general relative value of the importance to supply, between ecosystem components. It can also provide relevant information, for example, for scenarios testing or for use within risk assessment contexts as demonstrated by Culhane et al. (this issue). Moreover, the potential to supply dimension in the ESS score can also be calculated using real ecosystem services supply indicators, if data of interest is available. Dimensions 2 and 3, together, build on the concept of carrying capacity (Epstein et al., 2016). They are important to confer a realistic valuation property to the ESS score and may be used where

more detailed information is available and to test prospective management scenarios associated with specific EBM measures.

Importantly, the presented approach does not aim to substitute a proper ES quantification, but can help to provide a simple proxy of the relevance of an ecosystem component for ecosystem services provision. In this sense, there are critical assumptions in the score, for example related to the weights of the three dimensions proposed here, that can be adjusted to ensure that they reflect the desired importance (Becker et al., 2017). These weights should be discussed with stakeholders and their sensitivity tested in the context of real applications. In addition, societal perspective also matters when weighting each dimension (Cherchye et al., 2008), for example regarding the level of flexibility for defining environmental objectives or conservation targets, regarding the value attributed to the services delivery potential or even on baseline services valuation. Nonetheless, we consider that this score provides valuable complementary screening information and allows tracking progress regarding both ES provisioning and biodiversity conservation.

4.4. Uncertainty

Three main sources of uncertainty have been identified that influence the outcome of the assessment: 1) the classifications adopted for categorizing EC; 2) the variability in experts' valuation of the links; and 3) the aggregation procedure. We address each of these aspects according to the nature of the information and the data available, to discuss their impacts in the final ES Supply outcome.

The effect of the heterogeneity of habitats across realms needs to be acknowledged, when comparing across realms and when scaling-up or aggregating weights. This is partially due to differences in the EUNIS scheme regarding the level of detail within the same EUNIS level to describe different ecosystem components (i.e. habitats). Freshwater habitats, in particular those within the realms lakes and rivers, are described more generally than coastal and marine habitats although at the same EUNIS level 3 resolution. This may lead to an underestimation of the ES supply potential of freshwater ecosystems and to an inadequate discriminant capacity of the components most linked to particular ES in freshwaters, as all services tend to be lumped at broad habitat descriptions.

In addition to inconsistencies in the habitats classification schemes, it is also acknowledged that accounting for mobile biotic groups separately from habitats may underestimate the real contribution of habitats to a given a service. To overcome this, the ES directly provided by highly mobile biotic groups were added to the habitats to which the groups are known to be associated across their life cycle. In this study however, we did not discriminate if all the ES provided by a given biotic group were differently associated with different habitats because we used mobile biota at a very broad taxonomic scale. If better resolution information would be available, this aspect should be accounted for in future assessments.

Using an expert judgement approach for evaluating the complex relationships between biodiversity and ecosystem services also increases the uncertainty associated with the linkages valuation. The differences in the valuations could be a result of a combination of factors, namely a) differences in normative interpretations, since the concepts 'weak' or 'strong' contribution to an ES are qualitative notions that not translate necessarily into perfectly equivalent assessments; b) differences in the levels of local knowledge across CS due to expertise level and/or regional available information; or c) differences in the CS themselves, since different conservation status or environmental condition may alter the perception on habitats' inherent value. Also, the use of a rating approach must acknowledge and deal with the limitations of extreme cases where a unique habitat unit is reported by only one CS, not allowing for a consistent evaluation. Nonetheless, given the high consistency found between expert valuations in the multiple-assessed units, some confidence can be attributed to single expert valuations.

Finally, the aggregation procedures, i.e. approaches for computing one score for several reported links, may also influence the final output, for example using weighted or non-weighted estimates, or using a more precautionary (e.g. maximum observed scores) versus a conservative approach as used in our analysis (e.g. mean scores). Choice should attend to purpose and application of study as well as baseline data.

5. Conclusions

One of the added values of this comprehensive linkage framework is its application potential. The consistency found in expert valuations across aquatic realms from a wide geographical range strongly underlines the potential for this knowledge transfer. Further case studies on aquatic ecosystems elsewhere and their related ecotones can apply this linkage matrix to create expectations on the ecosystem services potential present in the given systems. The biodiversity–ecosystem services linkages are part of a broader framework that connects social and ecological systems and, thus, the supply and demand side of ecosystem services. The demand-side characterizes human activities and related pressures that are associated to aquatic environments allowing for an impact risk assessment (Borgwardt et al., 2019) and risk to supply assessment (Culhane et al., this issue). The full linkage closes a circle aiming to be a tool to support ecosystem based management of aquatic ecosystems (available online [AquaLinks database](https://aqualinksdatabase.com), 2018).

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Appendix A. Supplementary data

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