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Ecosystem Science
for Policy & Practice

This project has received funding from the European Union's Seventh Framework Programme for research, technological development and demonstration under grant agreement number 308393.

Prepared under contract from the European Commission
Project reference: 308393
Collaborative project
FP7 Environment

Project acronym: **OPERAs**
Project full title: **Operational Potential of Ecosystem Research Applications**
Start of the project: 1 December 2012
Duration: 60 months
Project coordinator: The University of Edinburgh
Project website: operas-project.eu

Deliverable title: Transferable geo-referenced metrics and GIS based quantification functions - *Pathways to the incorporation of biodiversity into ecosystem service biophysical assessment*.
Deliverable number: 3.1
Nature of the deliverable: Report
Work package responsible: WP3
Partner responsible: Sandra Lavorel
Other partners involved: Sandra Lavorel, Almut Arneth, Anita Bayer, Alberte Bondeau, Sven Lautenbach, Nuria Marba, Ana Ruiz, Nynke Schulp, Ralf Seppelt, Astrid van Teeffelen, Clémence Vannier, Peter Verburg
Due date of deliverable: Month 18
Actual submission date: Month 18
Deliverable status:

Version	Status	Date	Authors
1.0	Draft	28 May 2014	Sandra Lavorel, CNRS

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Brief description of Deliverable 3.1:

Initial set of transferable geo-referenced metrics, and GIS based quantification for ES/NC. The deliverable contains a selection and description of the ways in which in operational research (e.g. in the exemplars) the links between biodiversity and ES can be established. It will identify which metrics for both biodiversity and ES quantification are recommendable for use in exemplar studies (and beyond). One chapter will document the quantification methods for marine ecosystem services

Abstract

While the mapping of ecosystem service supply has become quite common in ecosystem service assessment practice for terrestrial ecosystems, land cover is the most common indicator used in so-called spatial proxy, GIS models of ecosystem service supply. For marine ecosystems, practice is even less advanced, with a clear deficit in spatially-explicit assessments of ecosystem service supply. This situation contrasts with increasing understanding of the role of terrestrial and marine biodiversity for ecosystem functioning and thereby for ecosystem services. This deliverable aims to address this gap by providing a synthesis of available approaches, models and tools, and data sources to parameterise them (in Europe), in order to better incorporate the role of biodiversity for ecosystem service supply into ecosystem service assessments, planning and natural resource management. Based on a review of published models, and ongoing developments in OPERAs WP3, models and associated geo-referenced metrics are classified according to the way in which biodiversity is represented, with five types of models: proxy-based, phenomenological, macro-ecological, trait-based and processed bases. Examples from models available in OPERAs and in the literature are presented, and the current plans for implementation in OPERAS's Examplars are summarised. We then discuss available data sources for parameterising different facets of biodiversity (species, phylogenetic, functional) in spatially-explicit models of ES supply, and the promises held by remote sensing. We end with aspects on the assessment of model uncertainty and validation. The last part of the discussion is dedicated to pathways for mapping of marine ecosystem services, a currently large gap in available methods, while a great scientific and societal challenge.

1. Introduction

The question of the spatially-explicit quantification of ecosystem services using geo-referenced metrics and GIS-based approaches has recently gained prominence through on the one hand the needs from policy and decision-makers for global to local assessments (Maes *et al.*, 2012), and on the other hand the emerging practice of land planning (von Haaren & Albert, 2011) or land management decision (e.g. in agriculture or forestry, (Doré *et al.*, 2011, Grêt-Regamey *et al.*, 2013, Soussana *et al.*, 2012)) that incorporates ecosystem services among land use allocation and land management criteria.

As a result mapping ecosystem services appeared as relatively common in the period of the investigation of Milestone 2.3 (2011 – Aug. 2013), where nearly a third of the studies were found to map ecosystem services (regardless of category). The percentage of studies mapped per ecosystem service category is relatively stable across the different categories (Figure 1, Table 1) – categories which are mapped less frequently are biochemical products and medicinal resources (P5), ornamental species (P7), Water quality regulation (R4), biological regulation (R7) and nutrient cycling (S3). The models behind ecosystem service mapping can be quite different (Figure 2): half of the mapping studies are based on relatively simple lookup table approaches while GIS models. The use of the different model categories to map ecosystem services differs by ecosystem service category. Process models are not used to map most cultural service. A relatively high share of studies use process models to map climate regulation (R2) and erosion control (R5) as well as for food (P1) and fuel und fibre provisioning (P3) (Figure 3 - Number of studies that mapped ecosystem services grouped by the main modeling categories and by ecosystem service categories.).

Linked with this increased practice of ES mapping, several recent reviews have summarised methods used to map ES. (Crossman *et al.*, 2013b) asserted that : 'the inconsistency in methods to quantify and map ecosystem services challenges the development of robust values of ecosystem services in national accounts and broader policy and natural resource management decision-making'. In Australia, (Plant & Ryan, 2013) identified the lack of an 'ES toolbox' as a barrier to the adoption of ES by natural resource managers. Further, in the case of marine ecosystems, ES quantification is not as well-developed all together, and its progress is a priority (Maes *et al.*, 2012). (Martinez-Harms & Balvanera, 2012) found that in international literature published until 2011, regulating services were the most commonly mapped, followed by provisioning services. Biophysical data (land-cover variables) were most commonly combined with mixed sources (databases like global statistics) as secondary (rather than primary – see also Seppelt et al. 2011) data. The most commonly used method to model services was the development of models based on the well-known causal relationships between environmental variables, followed by the extrapolation of ES values from primary data to the total analysed area, frequently using land-cover maps. They concluded that: '*There is an urgent need to develop methods for deepening our understanding of the social–ecological processes behind the supply of ES in order to* *improve our ability to map ES for decision making*', a need further elaborated by (Nagendra *et al.*, 2013).

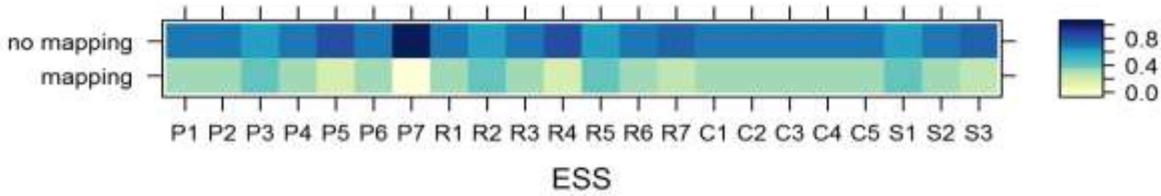


Figure 1 - Mapping of ecosystem services for the different ecosystem service categories. Values have been normalized by ecosystem service category. The abbreviations are explained in Table 1.

ID	Ecosystem Service
Provisioning	
P1	Food
P2	Fresh Water: storage and retention of water; provision of water for irrigation, industry and for drinking.
P3	Fibre & Fuel & other organic raw materials: production of timber, fuel wood, peat, fodder, aggregates
P4	Inorganic resources (oil, minerals, etc) "Geological services"
P5	Biochemical products and medicinal resources:
P6	Genetic Materials: e.g. genes for resistance to plant pathogens
P7	Ornamental species: e.g. aquarium fish and plants, shells, etc
Regulating	
R1	Air quality regulation: (e.g. capturing dust particles
R2	Climate Regulation: regulation of greenhouse gases, temp., precipitation, and other climatic processes
R3	Water quantity regulation (e.g. ground-water recharge/ discharge; surface flow regulation, storage of water)
R4	Water quality regulation (e.g. waste treatment) retention, recovery and removal of excess nutrients / pollutants
R5	Soil retention and erosion protection
R6	Natural Hazard mitigation/ disturbance regulation : flood control, storm & coastal protection
R7	Biological Regulation: e.g. control of pest-species and pollination
Cultural & Amenity	
C1	Cultural heritage and identity: sense of place and belonging
C2	Spiritual & artistic Inspiration: nature as a source of inspiration for art and religion
C3	Opportunities for tourism and recreational activities
C4	Aesthetic: appreciation of natural scenery (other than through deliberate recreational activities)
C5	Science & Educational services opportunities for formal and informal education & training
Supporting	
S1	Biodiversity & nursery: Habitats for resident or transient species.
S2	Soil Formation: sediment retention and accumulation of organic matter
S3	Nutrient Cycling: storage, recycling, processing and acquisition of nutrients

Table 1 - List of ecosystem service categories used in the analysis

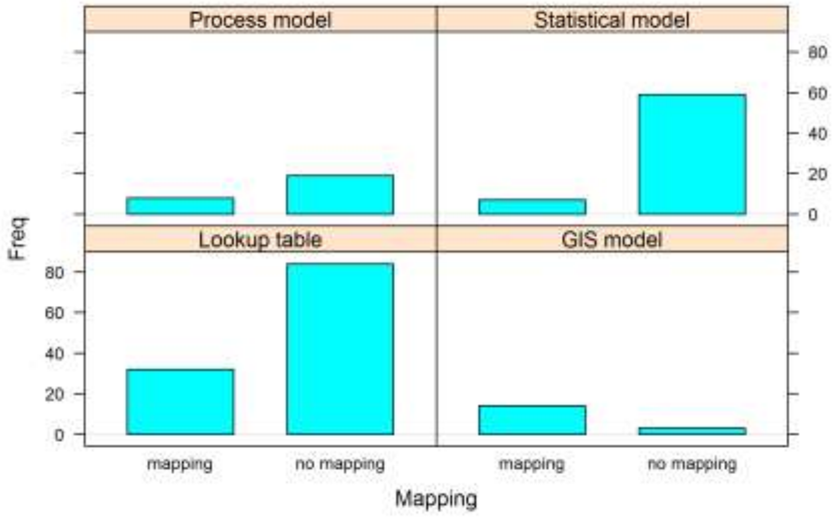


Figure 2 - Mapping of ecosystem services by the main modeling categories. Lookup table approaches refer to phenomenological models that use simply land use categories to estimate ecosystem services. GIS models refer to phenomenological models of higher complexity.

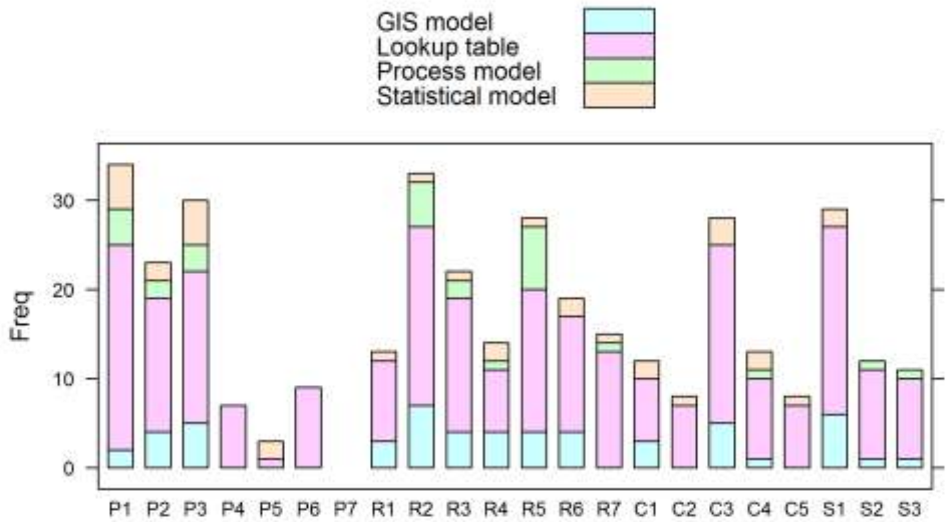


Figure 3 - Number of studies that mapped ecosystem services grouped by the main modeling categories and by ecosystem service categories.

(Egoh *et al.*, 2012) reviewed indicators available for the mapping of ES in Europe to address Action 5 of the European Biodiversity Strategy, requiring national-level mapping assessments by all member states, and the associated practice. Consistent with (Martinez-Harms & Balvanera, 2012, Seppelt *et al.*, 2011a) and Milestone 2.3, a majority of mapping studies addressed regulating services, followed by provisioning services. Simple proxy methods remained the most commonly used method for mapping ES, despite their highest potential error, especially when this proxy is land cover. They argued that, in spite of the need for models combining multiple indicators and data sources, because 'complex models require sound knowledge, data, and methodological approaches to describe the processes underlying ES supply', their uptake for practice might be limited. A large variety of primary indicators are currently used to express one single ES. This makes ES maps of different studies difficult to compare.

For terrestrial ecosystems, land cover is the most common indicator in practice (Egoh *et al.*, 2012), although this leads to severe uncertainty from national (Eigenbrod *et al.*, 2010) to landscape (Lavorel *et al.*, 2011) scales. More advanced models incorporate effects of above- and sometimes below-ground biomass, along with vegetation type, and soil parameters including nutrients, while even for cultural services, actual biodiversity data is rarely use. This contrasts with increasing understanding of the role of biodiversity for ecosystem functioning (Cardinale *et al.*, 2012).

This deliverable aims to address the need to bridge this gap by providing a synthesis of available approaches, models and tools, and data sources to parameterise them (in Europe), in order to better incorporate the role of biodiversity for ecosystem service supply. Based on a review of published models, and ongoing developments in OPERAs WP3, models and associated geo-referenced metrics are classified according to the way in which biodiversity is represented. Examples from models available in OPERAs and in the literature are presented, and the current plans for implementation in OPERAS's Examplars are summarised. We then discuss available data sources for parameterising different facets of biodiversity (species, phylogenetic, functional) in ES models, and the promises held by remote sensing. We end with aspects on the assessment of model uncertainty and validation. The last part of the discussion is dedicated to pathways for mapping of marine ecosystem services, a currently large gap in available methods (Maes *et al.*, 2013c), while a great scientific and societal challenge.

2. Classification of models for mapping ecosystem service supply

2.1. Methods

We reviewed ES biophysical modelling approaches available in OPERAs and in the published literature that incorporate more or less refined descriptions of biodiversity and its effects on ES supply. Models and associated geo-referenced metrics were classified according to the way in which the relationships between biodiversity and biophysical processes are represented: spatial proxy models, phenomenological models, macro-ecological models, trait-based models, and process-based models (Figure 4- Biodiversity components incorporated into different categories of models).

For each category of models we provide a standard description, including: a definition, a brief description of the principles and mechanics of application of these models (with special reference to GIS applications), an explanation of how biodiversity effects are represented and a specification of scales of applicability. This is followed by a short summary of example applications in OPERAs and in the literature, supported by standard model descriptions presented in Appendix 1. Lastly, key data sources and strengths and weaknesses for practice are discussed.

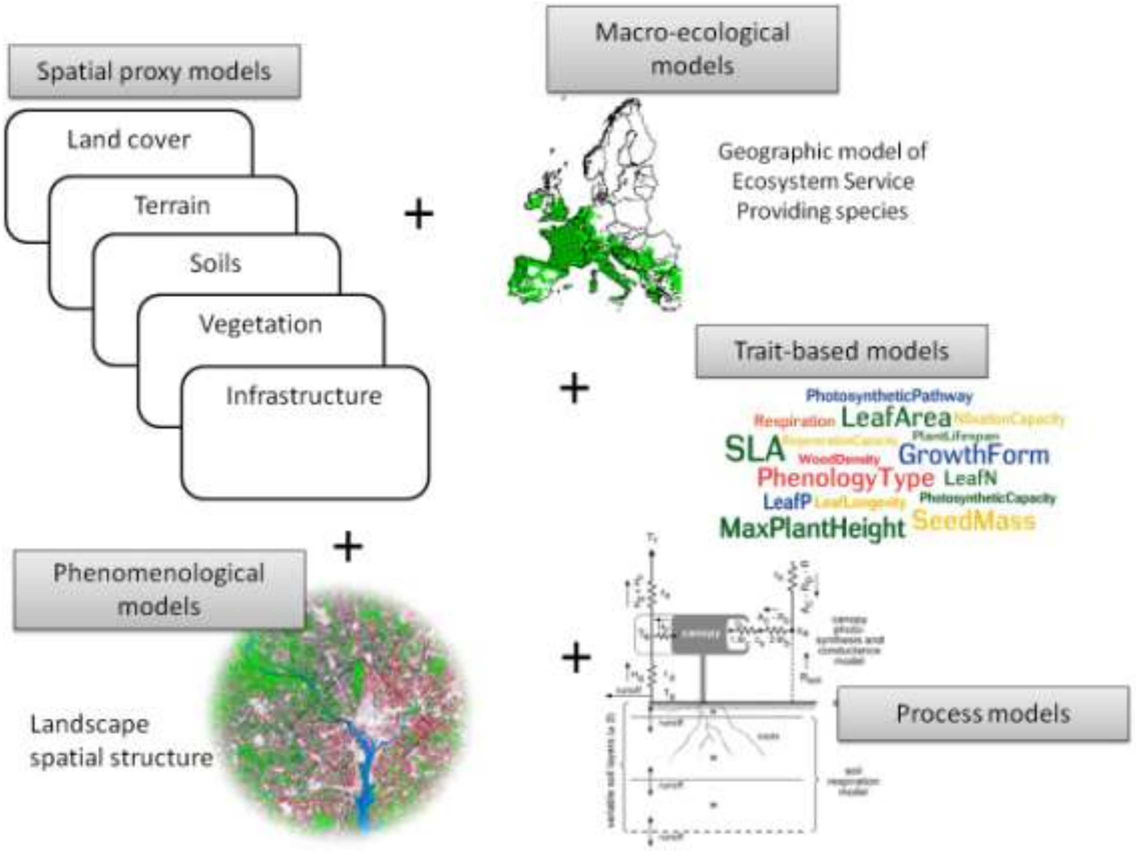


Figure 4- Biodiversity components incorporated into different categories of models of ecosystem service supply.

2.2. Spatial proxy models

2.2.1. Definition

We define spatial proxy models as models that relate ES indicators to land cover, abiotic and possibly biotic (although not often used beyond vegetation type) variables by way of calibrated empirical relationships. As such they therefore provide the most basic form of incorporation of 'biodiversity' effects on ES supply. It is desirable, and in practice most common for such models to be derived from well-known causal relationships between environmental variables (see (Martinez-Harms & Balvanera, 2012)).

2.2.2. How they work

Spatial proxy models are developed by statistical downscaling of land-cover based models. They use relations between ecosystem services and proxies for which spatial data are available determined by statistical or expert-based techniques (Kienast *et al.*, 2009). Biodiversity effects are represented by a statistical allocation of ES indicators depending e.g. on vegetation type or (more rarely) species composition, and a set of land use and environmental variables (e.g. altitude, soil type, climate…). One simple, and often used method consists in combining data layers with look-up tables allocating ES values per land cover and possibly according to modifying variables describing abiotic factors and ecological integrity considered in a categorical fashion (Burkhard *et al.*, 2012). Statistical models of varying complexity, developed from observations or analysis of regional data sets, may also be applied, representing 'Tier 2' approaches under the MAES suggested methods (Maes *et al.*, 2014), from multiple regression to more advanced models including Generalized Additive Models (Yee & Mitchell, 1991) or more sophisticated methods for capturing uncertainty in relationships, such as Bayesian modelling (Grêt-Regamey *et al.*, 2013).

2.2.3. How are biodiversity effects on ES represented

In spatial proxy models biodiversity is represented by habitat type (or biotope) or (more rarely) species composition. The most common examples use vegetation types, which are associated with levels of ES supply. This may range from the use of coarse vegetation types (e.g. evergreen vs. deciduous forest) to detailed habitat types such as those of the Habitat Directive. Likewise, for marine ecosystems different habitat types depending on bathymetry or substrate may be used to model ES associated with the presence or activity of particular species.

2.2.4. Scales of applicability

In general, uncertainty increases at smaller extents and greater resolution if the statistical models have been developed at larger scales. Site-specific models may be developed based on field collection (as encouraged by (Martinez-Harms & Balvanera, 2012) – see (Lavorel *et al.*, 2011))

2.2.5. Some examples

The commonly used platform InvESt (Nelson *et al.*, 2009) applies spatial proxy modelling for ES such as carbon sequestration. Here, annual production data are combined with specific expansion factors per vegetation types and a quantification of soil carbon stocks in order to estimate and map carbon sequestration in different habitats. (Schirpke *et al.*, 2013) combined past, current or future modelled maps of vegetation types in the Austrian Stubai valley with measures of ecosystem services such as fodder quantity and quality, carbon sequestration, soil stability and natural hazard regulation or aesthetic value. In the case of traditional forest landscapes of Lapland, (Vihervaara *et al.*, 2010) illustrated how multiple biophysical and social data sources can be combined to quantify regulation service supply by different biotopes. Advanced categorical models have been applied to estimate potential supply of woody biomass from the forests in the European Union (EU), by modulating potential production based on regional forest statistics (EFISCEN model) with multiple environmental, technical and social constraints (Verkerk *et al.*, 2011).

For the marine environment (Liquete *et al.*, 2013b)developed a proxy-based model to assess coastal protection at European level. The study provides a conceptual and GIS based methodological approach based on 14 biophysical and socioeconomic variables from terrestrial and marine datasets to assess coastal protection at different spatial-temporal scales. Variables were used to define three indicators: coastal protection capacity, coastal exposure and demand for protection. The indicators were subsequently framed into the ES cascade model to estimate how coastal ecosystems provide protection.

2.2.6. Data sources

Land cover (and especially CORINE in Europe), terrain, vegetation and soil layers are most commonly used here for terrestrial ecosystems. In marine ecosystem data layers indicating bathymetry, habitat distribution, sediment type, wave and currents regime, tidal range, water temperature are most frequently used.

2.2.7. Strengths and weaknesses for practice

Sophisticated proxy based models have been recommended for national assessment of ecosystem services (Maes *et al.*, 2014). They help move from a pure 'benefit transfer' approach based on land cover (Eigenbrod *et al.*, 2010) (MAES Tier 1), to more precise assessments (MAES Tier 2) using classic GIS methods accessible to all (Kienast *et al.*, 2009). Also, they can be easily combined with socio-economic variables in order to provide at least first level assessments of benefits (Burkhard *et al.*, 2012, Grêt-Regamey *et al.*, 2008, Vihervaara *et al.*, 2010). Model applications are however constrained by the availability of different data layers depending on scales / regions. For instance, while effects of soil parameters on regulation services (e.g. C sequestration, erosion control) are well understood by scientists and practitioners, soil maps are often not available at suitably fine resolution. A further weakness of simple statistical models lies in the uncertainty associated with projections of statistical relationships for future scenarios whose conditions exceed those under which models were developed (Figure 5 - Example of simple statistical modelling for wood production in the French Alps Examplar. Potential production was calculated by combining a map for distribution of forest types based on dominant species (source: IGN BD Forêt v2) with inventory data on production per forest type (IFN)).

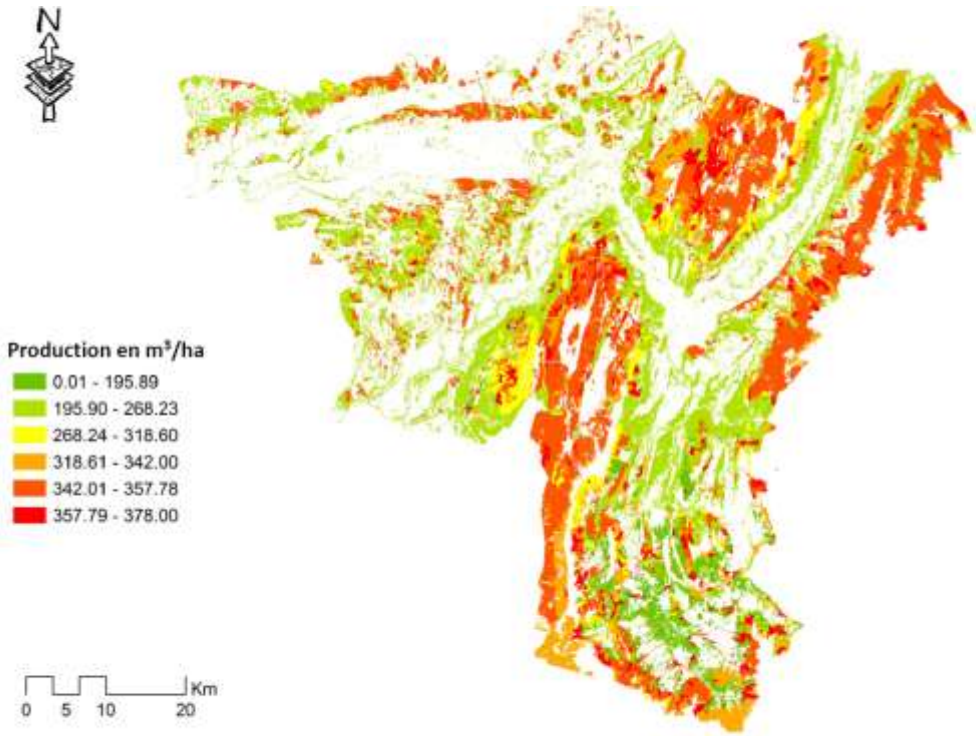


Figure 5 - Example of simple statistical modelling for wood production in the French Alps Examplar. Potential production was calculated by combining a map for distribution of forest types based on dominant species (source: IGN BD Forêt v2) with inventory data on production per forest type (IFN)

2.3. Phenomenological models of ecosystem services

2.3.1. Definition

Phenomenological models are based on qualitative or semi-quantitative relationships between biodiversity components and ES supply, based on an understanding of biological mechanisms underpinning ES supply.

2.3.2. How they work

Phenomenological models assume a relationship between elements of the landscape – quite often represented by land cover or land use classes – and the provisioning of and/or the demand for ecosystem services. This relationship might be represented by a simple lookup table of land cover classes, by a functional relationship between landscape attributes and services or might involve spatial configuration as well. A simple approach might assign a similar value to each forest patch of similar size. The value of each forest patch might also depend on additional attributes such as the soil quality or it might depend on its configuration (protection against avalanches depends heavily on the location of the forest with respect to steep slopes as well as with respect to built-up areas and infrastructure). In difference to purely empirical approaches parameters (or a part of the parameters) are not derived from observed data from the location of the model application. Instead parameters are transferred from other studies or meta-analysis.

2.3.3. How are biodiversity effects on ES represented

Biodiversity might be represented by changing the amount of service provided as a function of biodiversity - (Grêt-Regamey *et al.*, 2014) provides an example of such an approach in which connectivity is as a proxy to describe a biodiversity – ecosystem service relationship of dry meadows. Biodiversity indicators might be also used to derive service values, i.e. by assuming a relationship between plant or bird species richness and recreational value of a location. However, indicators related to biodiversity are not very commonly used in this type of models that are often dominated by the influence of the land use type.

2.3.4. Scales of applicability

Typically, these approaches are used at the regional to the global scale since the assumed relationships ignore most often smaller scale details and focus on patterns emerging at coarser scales.

2.3.5. Some examples

Pollination as an important ecosystem service (Klein *et al.*, 2007) that has to incorporate land use configuration has been modelled in a number of spatial explicit approaches. The approaches so far focused on the pollination of crops used either agriculturally or as wild food. The approach by (Lautenbach *et al.*, 2012b) focuses on the demand side of the service. Based on maps of crop yields of pollination dependent crops the benefits of the service were estimated. The work by (Grêt-Regamey *et al.*, 2014, Lautenbach *et al.*, 2011, Maes *et al.*, 2011, Schulp *et al.*, 2014a) models the demand for pollination together with the supply of the service represented by habitats suitable for wild pollinators (Figure 6 – Phenomenological model used to determine the visitation probability as a proxy for the pollination service. Adapted from (Schulp *et al.*, 2014a)). While these approaches relied on expert models to assess the suitability of pollinator habitats, habitat suitability would preferably be estimated by species distribution models if sufficient data is available (Polce *et al.*, 2013). Using results from a meta-analysis by (Ricketts *et al.*, 2008) the studies incorporate realized pollination as a decay function based on the distance between pollinator habitat and fields with pollination dependent crops. (Lautenbach *et al.*, 2011) used a k-nearest neighbour approach that limits the number of cells that could be pollinated by pollinator source cell while the other approaches did not limit the number of cells that could be pollinated by source cell. (Grêt-Regamey *et al.*, 2014) used knock-off thresholds based on connectivity to incorporate habitat quality indicators based on landscape configuration. (Lonsdorf et al., 2009) – on which the InVEST crop pollination model is based - include not only the location of crops to be pollinated and the habitat quality into their model but also the availability of floral resources, incorporating thereby implicitly biodiversity effects. The InVEST model offers the possibility to run the model using specific parameter values for different pollinator species or guilds. Examples for phenomenological assessments of other ecosystem services can be found in (Lautenbach *et al.*, 2011) for water quality regulation and recreation, in (Schulp *et al.*, 2008) for climate regulation through carbon sequestration, and for a large number of services in (Maes et al., 2011). In the Swiss valley of Davos, the cultural service of habitat for the protected bird species Capercaillie was modelled by combining habitat suitability criteria relating to quality and spatial pattern with GIS-modelled vegetation distribution (Grêt-Regamey *et al.*, 2008). The universal soil loss equation (USLE) and related approaches (Wischmeier & Smith, 1978) represents an example of phenomenological approaches which is commonly thought of as a process model, and has been used for the quantification of the ES of erosion control (Schirpke *et al.*, 2013).

In coastal environments phenomenological models are commonly used to assess services such as coastal protection. An example for wind protection by mangroves can be found in Das & Crepin 2013, where it was found that mangroves attenuate damage from cyclonic wind by providing protection to properties, even far away from mangroves and the coast. They devised a theoretical model of wind protection by mangroves and calibrated and applied this model using data from the 1999 cyclone in Odisha (India). Temmerman et al

2012 used phenomenological models to predict flood attenuation by tidal marshes and demonstrated that tidal marsh die-off, which may increase with climate change, is expected to have non-linear effects on reduced coastal protection against flood waves.

2.3.6. Data sources

Most approaches rely on land cover / use data as the primary data source. Depending on the service additional data may be used to represent the moderating factors of service supply. These may include soil conditions, climate conditions or the accessibility of areas. For a model of rural tourism supply in Europe (van Berkel & Verburg, 2011) used spatial data on land cover, topographic and terrain information, climate, protected areas and registration of local products as proxy for the 'sense of place'.

2.3.7. Strengths and weaknesses for practice

These approaches depend on the validity of the qualitative or semi-quantitative relationship. Typically, the required parameters are not available for a specific case study region and have to be transferred from other study sides. So results should be interpreted as indicators of the direction of an effect or of the relative importance of an effect (e.g. by comparing different land use scenarios or historic land use data) and not be misinterpreted as absolute values. The strength of the approach is that it allows the incorporation of land use configuration effects while requiring only a limited amount of data. It can therefore be used to get first estimates at regions or scales where data availability is limited or for the assessment of past conditions for which required data for more sophisticated approaches will not become available.

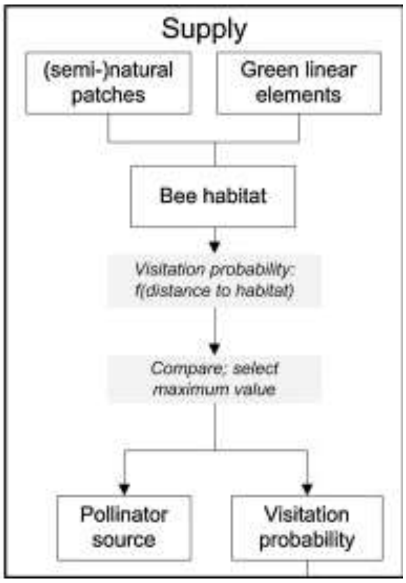


Figure 6 – Phenomenological model used to determine the visitation probability as a proxy for the pollination service. Adapted from (Schulp *et al.*, 2014a).

2.4. Macro-ecological models for mapping ecosystem services

2.4.1. Definition

We define as macro-ecological models of ES, models that assess ES supply based on the presence (or abundance) of specific components of biodiversity, referred to as Ecosystem Service Providers (ESP) or Ecosystem Providing Units (Luck *et al.*, 2009), depending on their geographic distribution. The contribution of e.g. different species or functional groups to the ES of interest is assessed based on specific traits (e.g. trophic guilds) or expert knowledge.

2.4.2. How they work

Macro-ecological models of ES are based on species-distribution modelling (Elith & Leathwick, 2009, Guisan & Thuiller, 2005), which can be a specific type of simple statistical modelling – though not only. Species Distribution Modelling (SDM) is based on the modelling of relationships between observed species occurrence and environmental parameters over geographic areas. Over the last two decades a wealth of SDM methods and applications have been developed, mainly in response to questions on global change impacts on biodiversity (Bellard *et al.*, 2012), but also with the prospect of using such models for biodiversity conservation (Guisan *et al.*, 2013). In essence, these methods produce statistical relationships that predict the probability of occurrence of a given species (or group of species) depending on parameters such as climate, soil or land use, and generate continuous distribution maps of these taxa. There are also more sophisticated, mechanistic models, which (akin to process models – see below) model species distributions based on physiological mechanisms (e.g. temperature tolerance thresholds, temperature responses), phenology (the timing of specific life cycle events such as bud burst or flowering in plants) or behaviour (for animals). Today several tools are freely available to facilitate modelling using a variety of methods (Maxent (Phillips *et al.*, 2006), BIOMOD (Thuiller *et al.*, 2009)). Once distributions of ESP, informed for instance through look up tables between biodiversity components and an ES of interest (e.g. vertebrate species and pest biocontrol) have been modelled then the ES is modelled by aggregation of maps for different ESP if there are more than one contributing species. In principle, any method of aggregation is possible, although so far applications have simply added contributing species without applying any weighting – i.e. considering the species richness for ESP as the proxy for the service.

2.4.3. How are biodiversity effects on ES represented

In macro-ecological models of ES, biodiversity effects are represented by aggregation of contributing species or other biodiversity components or parameters (e.g. number of species providing the service). For instance, in Mediterranean regions provisioning services such as timber, fuelwood or cork production may be related to the presence of particular species (e.g. *Fagus sylvatica* or *Quercus ilex*, or *Quercus suber* respectively) and to forest species richness (i.e. simultaneous occurrence of several species) (Vilà *et al.*, 2007), while spiritual and aesthetic values are supported by *Quercus suber* and *Pinus halepensis*, and the regulation of fire hazards is promoted by *Quercus suber* but negatively affected by *Pinus halepensis*. Though in their infancy, new approaches expand such species-based approaches by considering relationships between taxonomic, phylogenetic and functional diversity and their links to ES (Flynn *et al.*, 2011). Such approaches are built on the premise that since functional diversity, or functional composition tend to be better related to ecosystem service supply than species richness or diversity (Cardinale *et al.*, 2012), then macro-ecological models of species distributions could be combined with relationships between species and functional diversity in order to generate projections of ES. The incorporation of phylogenetic diversity, which can be easily computed based on taxonomic data granted the availability of phylogenetic data (e.g. (Thuiller *et al.*, 2011)), adds a further means to approach functional diversity and thereby to quantify ecosystem services (Cadotte *et al.*, 2009).

2.4.4. Scales of applicability

Macroecological models are suitable for regional to continental and global scale. Applications to smaller areas are problematic due to the omission of suitable environmental conditions outside of the study area.

2.4.5. Some examples

A macro-ecological approach was applied to model biocontrol of vertebrate and invertebrate pests by terrestrial vertebrates (birds, mammals, reptiles) in Europe, comparing current state and future climate change scenarios (Civantos *et al.*, 2012) (Figure 7 - Species distribution modelling method (a) and application to the modelling of biocontrol of invertebrate pests by vertebrates in Europe, quantified as the number of species with control potential under current conditions (b) and projected gains and losses by 2080 (Civantos et al. 2012)). This analysis showed that the pest control ES was likely to face substantial reductions, especially in southern European countries whose economies are highly dependent on agricultural yields. In much of central and northern Europe, where countries' economies are less dependent on agriculture, climate change was likely to benefit pest-control providers. (Schulp *et al.*, 2014b) used a similar approach to quantify the supply of wild foods across Europe and compare it with demand. Existing data bases of modelled species distributions for Europe may be used for other ES granted a relationship can be identified between the presence of particular species or species groups and ES supply. This may in particular apply to cultural services provided by well identified species (e.g. protected species, species of particular aesthetic value) or to provisioning by particular species such as in the case of wild foods.

In the marine environment the Ecopath with Ecosim (EwE) modelling approach can be used to predict changes in fish production. In particular EwE can be used to address ecological questions, evaluate ecosystem effects of fishing, explore management policy options, analyse impacts and placement of marine protected areas, predict movement and accumulation of contaminants and tracers and model the effects of environmental changes. Ewe has three main components: Ecopath (a static, mass balanced snapshot of the system), Ecosym (a time dynamic simulation module for policy exploration) and Ecospace (a spatial and temporal dynamic module for exploring impact and placement of protected areas. An example of the application of EwE can be found in Alcamo et al 2005, where fish consumption and production for three important regional marine fisheries (North Benguela, Central North Pacific and Gulf of Thailand) is modelled for the four global scenarios described under the Millennium Ecosystem Assessment (Global orchestration, Order from strength, Adaptative mosaic and TechnoGarden). This analysis showed that for all scenarios fish catch (by weight) is maintained in the North Benguela fishery, not maintained in the Central North Pacific, and has mixed results in the Gulf of Thailand. The overall message is that is not certain whether future demands of fish can be sustainably provided.

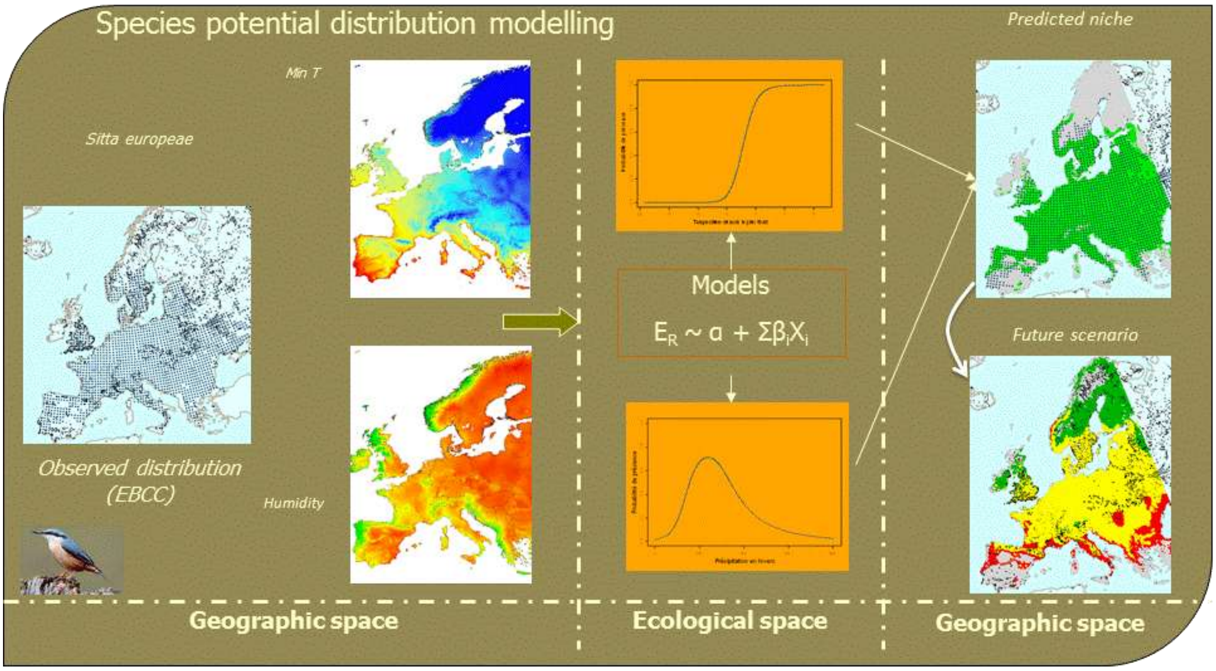
2.4.6. Data sources

SDM require as a primary ingredient species distribution maps. These may be available at regional (e.g. botanical or fauna inventories), national or European / continental scale (e.g. European Atlas of plant distributions, EFI atlas of tree distributions). Species distribution data are often the critical bottleneck for macro-ecological approaches. Environmental data layers are usually easier to acquire, though there should be a match between the resolution of species and environmental data. This in particular applies to climate, where downscaled layers need to be available or calculated for adequate distribution modelling. Conversely, care should also be taken in the use of high resolution maps, e.g. soil maps, which may be more accurate than available species locations.

2.4.7. Strengths and weaknesses for practice

Overall, macro-ecological modelling is a well-developed approach with free accessible tools, suitable for future scenario projections. The shortcomings of SDMs and strengths and weaknesses of different distribution modelling methods have been discussed extensively elsewhere (e.g. (Bellard *et al.*, 2012, Elith & Leathwick, 2009)), and we refer users to this literature for further details. Apart from the intrinsic limitations of the approach, such as ignoring population dynamics, species interactions, or potential adaptive responses, the main avenue for improvement towards the application to ES modelling regards the understanding and quantitative specification of relationships between biodiversity components and ES supply. This gap requires both greater ecological understanding about relationships between biodiversity components and ES supply (Cardinale *et al.*, 2012, Nagendra *et al.*, 2013), and research into the demand for ES in terms of the identities and relative weights of contributing species.

a



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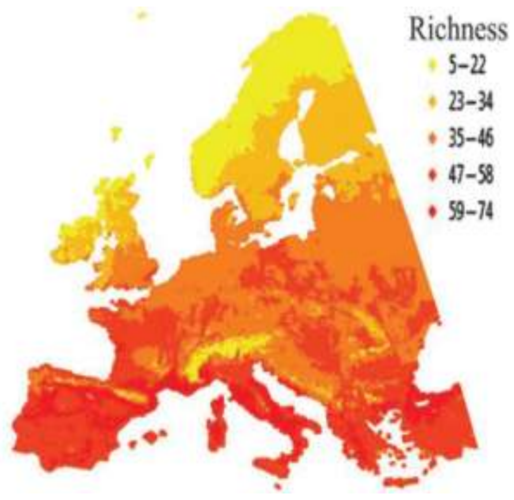

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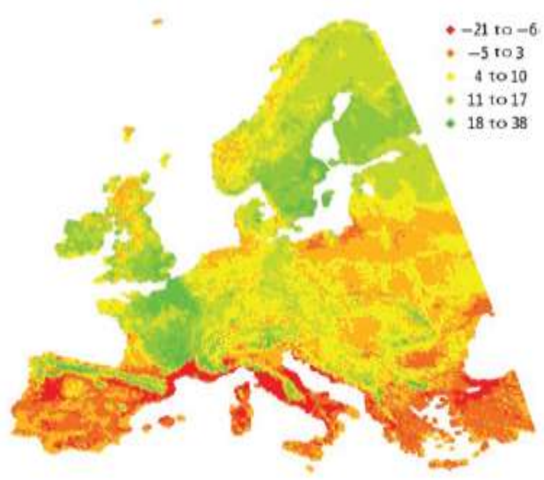

Figure 7 - Species distribution modelling method (a) and application to the modelling of biocontrol of invertebrate pests by vertebrates in Europe, quantified as the number of species with control potential under current conditions (b) and projected gains and losses by 2080 (Civantos et al. 2012)

2.5. Trait-based models for mapping ecosystem services

2.5.1. Definition

There is increasing evidence for relationships between traits of organisms and ES supply (De Bello *et al.*, 2010, Lavorel, 2013). Trait-based models quantify ES supply based on (statistical) relationships between functional traits of Ecosystem Service Providers (ESP) and ecosystem properties considered either by experts or by stakeholders to support a given ecosystem service (De Bello *et al.*, 2010, Luck *et al.*, 2009).

2.5.2. How they work

Trait-based models of ES are in their infancy and are based on the identification of statistical, quantitative relationships between an ecosystem property underpinning ES supply and trait-based metrics, as well as, if significant additional effects of abiotic parameters such as climate or soil variables (Gardarin *et al.*, 2014, Lavorel *et al.*, 2011). (Lavorel *et al.*, 2011) demonstrated that the accuracy of trait-based models exceeds that of models based on land use alone, or even land use and soil variables, thereby reducing their large uncertainties for regional, and a fortiori landscape applications (Eigenbrod *et al.*, 2010, Martinez-Harms & Balvanera, 2012). Such models are constructed based on empirical measures of ecosystem functioning, which are then related to explanatory variables including: land use / land cover, trait-based metrics quantifying functional diversity of ecosystem service providers (see below 'How are biodiversity effects represented' for details), soil variables and, for regional to continental scale or topographically complex landscapes climate / microclimate variables. In principle, and similar to macro-ecological models, a wide range of modelling methods are suitable (Elith & Leathwick, 2009, Thuiller *et al.*, 2009), although selected methods must allow spatially-extensive extrapolation over space for which explanatory variables are available (directly or from models), and preferably across time under scenarios. This latter criterion tends to exclude for instance neural networks of classification trees. Further, and although this has not been applied yet in the case of trait-based ES models, uncertainty associated with the choice of modelling method could be quantified (Thuiller *et al.*, 2009). Once ecosystem properties have been modelled, maps are generated by parameterising the models using land use, soil or climate layers (Lavorel *et al.*, 2011). Ecosystem service maps are then obtained either by equating the ecosystem property with the ES of interest, or by combining maps for several relevant ecosystem properties. For instance (Lavorel *et al.*, 2011) mapped the agronomic value of grasslands by combining modelled maps for three ecosystem properties: annual biomass production, fodder quality and the timing of flowering (given that delayed flowering maintains quality for longer and gives farmers flexibility for the harvest date). As in the case of macro-ecological models, criteria for the combination of multiple ecosystem properties have so far often been very basic (e.g. simple sum), although the sensitivity of final maps to relative weightings is highly significant (Gos & Lavorel, 2012). Here, more advanced criteria (i.e. weights) would need to be quantified based on social and/or economic valuation.

2.5.3. How are biodiversity effects on ES represented

Trait-based models quantify the effects of functional components of biodiversity on ecosystem properties of interest. These may include a variety of metrics that depict different dimensions of functional diversity such as functional richness (the number of trait values represented in the relevant ESP community), functional range (the extent trait values, e.g. min-max, represented in the relevant ESP community), functional evenness (the relative representation of trait values in the trait values represented in the relevant ESP community), or functional divergence or dissimilarity (an indication of the variance in trait values across the community) (Mouchet *et al.*, 2010). Models may be single or multi-trait, in the following two ways: 1) combination of single-trait metrics for several individual traits (e.g. plant height and leaf nitrogen concentration to model grassland productivity - (Lavorel *et al.*, 2011)); or 2) multi-trait metrics such as community weighted mean of a compound index of different traits (e.g. leaf economics spectrum - (Laliberté & Tylianakis, 2012, Lienin & Kleyer, 2012, Mokany *et al.*, 2008)) or multivariate divergence in a set of traits (e.g. (Conti & Diaz, 2013, Mokany *et al.*, 2008)). A review of known relationships between indicators of ecosystem biogeochemical functioning for plants, relevant to the modelling of ES such as for instance fodder or timber production, climate regulation through carbon sequestration or the maintenance of water quality, suggested that, for available studies so far, community mean values of single traits tended to capture most of the variance in these ecosystem properties (Lavorel *et al.*, 2013b). In addition, a conceptual breakthrough has been proposed to use multitrophic trait-based models to quantify ecosystem services resulting from the interaction between several trophic levels such as pollination, biotic control of pests and weeds or maintenance of soil fertility (Grigulis *et al.*, 2013, Lavorel *et al.*, 2013a). These models capture not only the effects of environmental change on ES via their effects on e.g.plant traits, but by also integrating the traits that underpin biotic interactions between plants and other organisms such as pollinators (Pakeman & Stockan, 2013), herbivores (Ibanez *et al.*, 2013), biotic control agents (Storkey *et al.*, 2013) or soil microorganisms (de Vries *et al.*, 2012, Legay *et al.*, submitted), and their effects of ecosystem service supply (Grigulis *et al.*, 2013, Moretti *et al.*, 2013, Orwin *et al.*, 2010).

2.5.4. Scales of applicability

Local to continental; particularly well-suited for local-landscape(-regional). See discussion on larger scale applications through remote sensing.

2.5.5. Some examples

Models of mountain grassland ES supply were developed based on plant traits (Lavorel *et al.*, 2011), and further complemented by traits of soil microorganisms (Grigulis *et al.*, 2013). In these models which focused principally on components of carbon and nutrient cycling, ecosystem properties were linked to plant height and easily measureable leaf traits such as dry matter content and nitrogen concentration, with additional effects of soil parameters. Both traits and soil parameters were related to grassland management to produce ES maps (Figure 8 – Schematic summary of modelling steps of ecosystem services based on cascading effects from land use and environmental variables, to community mean plant traits and to ecosystem properties, illustrated here in the case of fodder production by mountain grasslands (adapted from (Lavorel *et al.*, 2011) and (Lavorel & Grigulis, 2012)). These models see also applied to project effects of combined climate and socio-economic scenarios translated into grassland management projections and parameterised from observations and experiments (Lamarque *et al.*, 2014). Likewise, (Schirpke *et al.*, 2013) were able to model and project for future climate scenarios mountain slope stability depending on plant root depth and density.

2.5.6. Data sources

Trait-based models have similar requirements to other statistical spatial models of ES regarding land use / land cover, climate or soil data layers. Additional to these, their initial construction requires observational or experimental data sets measuring ecosystem properties underpinning ES supply along with at least community composition of ecosystem service providers. The latter can then be combined with original, site-level trait data, or data extracted from trait data bases, with due caution with respect to intraspecific trait variability (Kazakou *et al.*, 2013, Violle *et al.*, 2012), to calculate trait-based metrics with standardized packages (Casanoves *et al.*, 2011, Laliberté & Shipley, 2011). Scenario projections can be parameterised by combining projected values for land use and environmental parameters with new community-level trait values obtained by considering the joint effects of species compositional turnover based e.g. on state-and-transition models (Quétier *et al.*, 2007) and of intraspecific variability quantified either through measures along environmental gradients (Albert *et al.*, 2010) or through experiments (Jung *et al.*, 2014).

2.5.7. Strengths and weaknesses for practice

Although trait-based models of ES supply are in their infancy they rely on rapidly increasing conceptual and empirical evidence (Lavorel, 2013). For instance, an inventory of studies published until early 2013 revealed a total of 82 known relationships between components of plant functional diversity (community mean or FD metrics) and ecosystem properties relevant to carbon, water or nutrient cycling and associated provisioning and regulation services. The recent extension to ES associated with other biota such as soil fauna and microorganisms (Mulder *et al.*, 2013), insects (Ibanez, 2012, Moretti *et al.*, 2013), terrestrial vertebrates (Luck *et al.*, 2012), aquatic invertebrates (Engelhardt, 2006) or marine fish (Albouy *et al.*, 2013) holds high promises for a more mechanistic approach to ES modelling based on analysis of field observations, as recommended by (Martinez-Harms & Balvanera, 2012). Further, such models provide a mechanistic basis for the understanding of biophysical bundles and trade-offs in ES supply (Lavorel & Grigulis, 2012, Mouillot *et al.*, 2011). The existence of so called 'response – effects overlaps' (Lavorel & Garnier, 2002, Suding *et al.*, 2008) enable mechanistic ES projections under future scenarios using relatively simple models (Lamarque *et al.*, 2014). As with any statistical model however, the greatest care should be taken when attempting to apply such models beyond the parameter space for which they were derived. Beyond this temporal issue, so far trait-based ES models have not been validated across sites. Interestingly an examination of available plant trait-based models of grassland biomass production (Lavorel *et al.*, 2013b) highlight similar structures across models, with the contribution of plant height and leaf nutrient economics traits, and likewise for the consistent linkage between fodder digestibility and leaf nutrient economics traits. An inter-site analysis showed highly consistent links between fodder digestibility and leaf dry matter content across 14 French grassland sites, with only a constant additive effect of site mean annual temperature, similar to what had earlier been observed for litter decomposability across 9 European sites (Fortunel *et al.*, 2009). The fodder digestibility model has been applied to national scale to produce a spatially extensive map across all French semi-natural grasslands (Garnier *et al.*, 2013). Nevertheless such scaling exercises should be generalised in order to validate models developed from plot scale data for application at regional to continental scale. Lastly, trait-based models will become increasingly attractive as trait data bases become more generally available (see Discussion below), although the lack of soil data layers in many countries / regions will remain problematic.

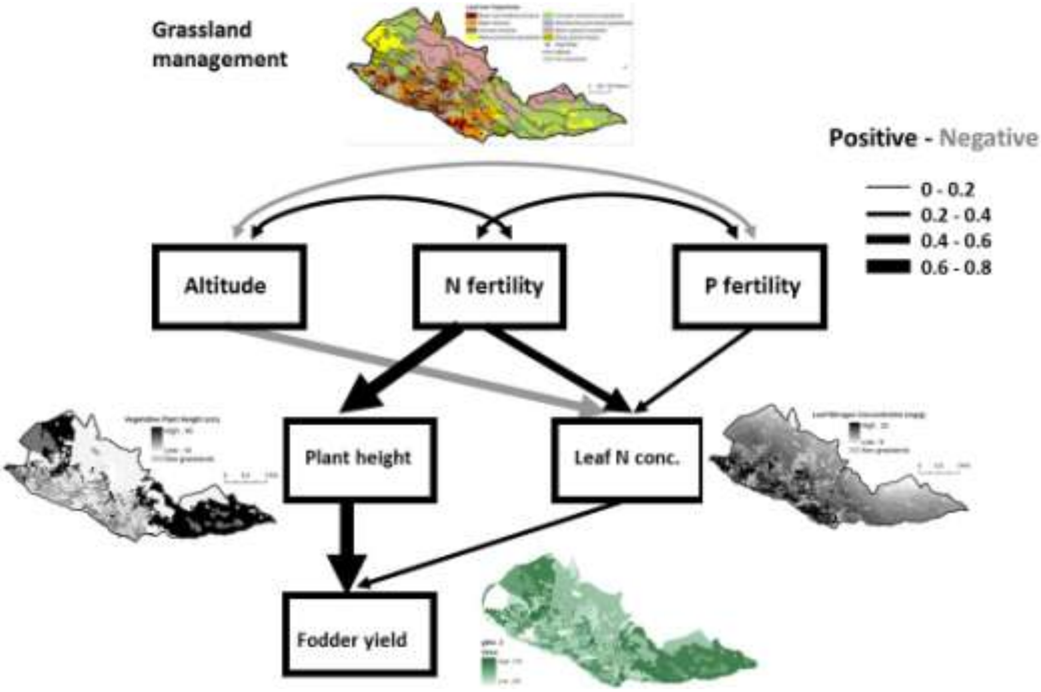

Figure 8 – Schematic summary of modelling steps of ecosystem services based on cascading effects from land use and environmental variables, to community mean plant traits and to ecosystem properties, illustrated here in the case of fodder production by mountain grasslands (adapted from (Lavorel *et al.*, 2011) and (Lavorel & Grigulis, 2012)).

2.6. Process-based models of ecosystem services

2.6.1. Definition

Process-based models rely on the explicit representation of ecological and physical processes that determine the functioning of ecosystems. Process-based dynamic vegetation models (DVMs) were developed as large-scale mathematical representations of biological systems that incorporate the current knowledge of physiological and ecological mechanisms at the process level into predictive algorithms. They provide functional means of plant and ecosystem processes that are universal rather than specific to one biome or region (Prentice and Cowling, 2013). One purpose of such models is to explore the impact of perturbations caused by climatic changes and anthropogenic activity on ecosystems and their biogeochemical feedbacks. Many process-based models allow the net effects of these processes to be estimated for the recent past and for future scenarios (Prentice, 2001). In terms of ecosystem services, these types of models are most widely applied to quantify climate regulation (Metzger et al., 2008; Naidoo et al., 2008; Ooba, et al., 2012; Watanabe et al., 2013), water supply from catchments (Gedney et al., 2006; Logsdon et al., 2013), food provision (Bateman et al. 2013) but also in the wider frame of habitat characterisation (Hickler et al., 2012; Huntingford et al., 2011).

2.6.2. How they work

Dynamic vegetation models simulate biogeochemical processes as a function of prevailing climate and atmospheric CO2 concentration and eventually in response to other inputs (e.g. land use, nutrient deposition). Model input may be prescribed (such as from observations) or be the output of climate models (Prentice, 2001). Vegetation is simulated as being composed of a quantitative mixture of plant functional types (PFT, see below), or species in the case of some forest models (Schumacher & Bugmann, 2006). Age or size classes may be distinguished, but more typically the modelled properties represent averages of the entire grid cell population of a given PFT (Prentice et al., 2007).

Many DVMs use a uniform set of process formulations to represent key biogeochemical processes (e.g. BIOME family of models see Fig. 1 for an example, (Haxeltine & Prentice, 1996). “Fast” processes are modelled on a daily basis and include energy and gas exchange, photosynthesis, respiration and plant-soil water exchange. Photosynthesis at the leaf level is modelled by the (Farquhar *et al.*, 1980) model or derivatives of it. Processes with seasonal dynamics such as plant phenology, growth and biomass allocation are implemented on a monthly basis. Carbon assimilated by each PFT (or species) is partitioned among its biomass compartments (leaves, roots, stems) according to fixed allocation coefficients (Prentice *et al.*, 2007). Population growth is the balance of an annual rate of establishment of new saplings and mortality. Carbon entering the soil as litter is transferred to multiple soil carbon pools with longer average decomposition times that are mainly governed by temperature and soil moisture (Prentice *et al.*, 2007). For soil water, the models usually consider a multi-layer scheme. Surface runoff is calculated as the balance between precipitation, water loss through transpiration by plants and evaporation. Several models include fire as natural disturbance, which is represented as feedback process with the vegetation state controlling the probability of burning and fire characteristics and other forms of natural disturbances (e.g. insect attacks, wind-throw) that are implemented stochastically.

Many DVMs take into account the direct manipulation of natural ecosystems by humans, e.g. by accounting for land-use or even detailed management (in the case of forests), or the limitation of plant processes by multiple nutrients (H2O, C, N, P). However, the treatment of these interacting processes varies widely (e.g. representation of management techniques, fertilization and irrigation).

2.6.3. How are biodiversity effects on ES represented

Vegetation cover is simulated using a small number of PFTs that are distinct in terms of bioclimatic limits and ecological parameters (see, e.g., (Lavorel *et al.*, 2011, Woodward & Cramer, 1996)). The PFTs represent a low-dimensional continuum of plant trait combinations. Process-based models therefore underestimate the functional diversity of communities in favour of a manageable number of classes that allow for high computational effectiveness.

2.6.4. Scales of applicability

Process-based models range from local to global application. Global models typically apply a spatial resolution of 0.5°x0.5° (e.g. LPJ-mL, LPJ-GUESS). The implemented processes are optimized for a certain scale and a scaling of the sub-components over space and time is possible in ranges that are similar to the original one.

2.6.5. Some examples

LPJ-GUESS DGVM (Sitch *et al.*, 2003, Smith *et al.*, 2001) simulates the development of land vegetation with an individual- and patch-based approach (Figure 9). Competition for resources and light among woody plant individuals in natural vegetation is simulated explicitly through gap dynamics, accounting for both age cohorts and height structure. The stochastic behaviour of many individual plants is simulated in multiple replicate plots. C-N coupling is incorporated for potential natural vegetation (see (Smith *et al.*, 2014, Wårlind *et al.*, 2014)). LPJ-GUESS incorporates a detailed representation of land use (Lindeskog *et al.*, 2013, Rosenzweig *et al.*, 2013), modelled using 11 generic crop functional types (CFT) that represent the most widely-grown crop species globally and their fractions explicitly given by land-use input. The LPJ-GUESS model has been evaluated extensively and has demonstrated skill comparable to other approaches in capturing dynamics of the terrestrial carbon cycle (e.g., (Morales *et al.*, 2005, Sitch *et al.*, 2013)). Within the OPERAs project, new approaches for adopting model output specifically for quantification of ES supply are being developed.

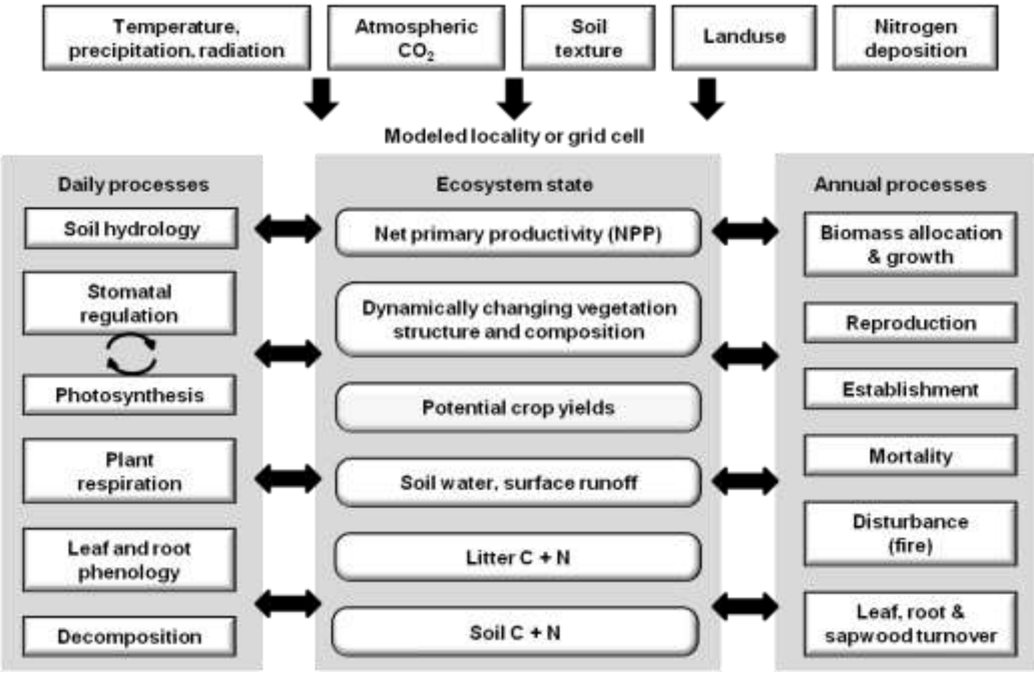

Figure 9 - Major processes within the LPJ-GUESS DGVM including features for nitrogen dynamics and land use representation (after Smith et al., 2001).

LPJmL (Bondeau *et al.*, 2007) is another development of the LPJ DGVM family (Gerten *et al.*, 2004, Sitch *et al.*, 2003). It runs using the population mode of LPJ DGVM, i.e. each plant functional type is represented by an average individual within the grid cell. It was especially developed for accounting for land use and land management: it uses 12 generic crop functional types, 3 types of managed grasslands, 3 bioenergy functional types (Beringer *et al.*, 2011, Rolinski *et al.*, 2010). It accounts for surface irrigation from rivers and reservoirs (Biemans *et al.*, 2011, Fader *et al.*, 2010, Rost *et al.*, 2008) and is part of the bio-economy modelling framework MAgPIE (Lotze-Campen *et al.*, 2008, Lotze-Campen *et al.*, 2010) used for land use modelling and integrated assessment. LPJmL has been validated for many aspects: phenology and crop yields (Bondeau *et al.*, 2007), CO2 fluxes (Jung *et al.*, 2008), trends in river discharges (Gerten *et al.*, 2008, Langerwisch *et al.*, 2013), sowing dates (Waha *et al.*, 2012) etc. The original version of the model (without land use) was used in the first continent-wide simulations of the vulnerability of ecosystem services in Europe under climate change (Schröter *et al.*, 2005). Since then, LPJmL (or LPJ DGVM) has been further developed to simulate various ecosystem functions and services, and their vulnerability or alteration under global change. Spatially explicit assessments have been made for crop yields, carbon sequestration, fire risk, biomass, flood risk, etc. (Müller *et al.*, 2009, Müller *et al.*, 2007, Müller *et al.*, 2014, Thonicke & Cramer, 2006).

The choice of management is a key factor in the adaptation capability of agro-ecosystems under climate change. LPJmL has already been used to quantify the global potential to increase crop production through changed water management in rain-fed agriculture (Rost *et al.*, 2009), and also the mitigation of yield losses in Sub-Saharan Africa through the more frequent choice of multiple cropping systems (Waha *et al.*, 2013). For using LPJmL in the Mediterranean Exemplar of OPERAs, 10 additional crop functional types are currently implemented for considering specific Mediterranean production systems, especially the perennial crops (Fader et al., in prep) (Figure 11 - Examples of LPJmL outputs for the Mediterranean exemplar.). Due to the recurrent water stress conditions of the Mediterranean agro-ecosystems and the increasingly severe projections of warming and rainfall decrease, innovative farming practices dealing with soil conservation and functional agrobiodiversity may offer improved management towards resilient agricultural systems. Their representation is currently implemented in LPJmL in order to be able to map the trade-offs between ecosystem services and related impacts (including aspects of landscape-level biodiversity) due to different management strategies, especially under climate change (Figure 10 shows the ecosystem services and related impacts that can be directly simulated by LPJmL (in blue). The combination with data from other sources for other variables (in brown) will allow a broader-spectrum trade-off analysis, especially under different management scenarios and climate change.).

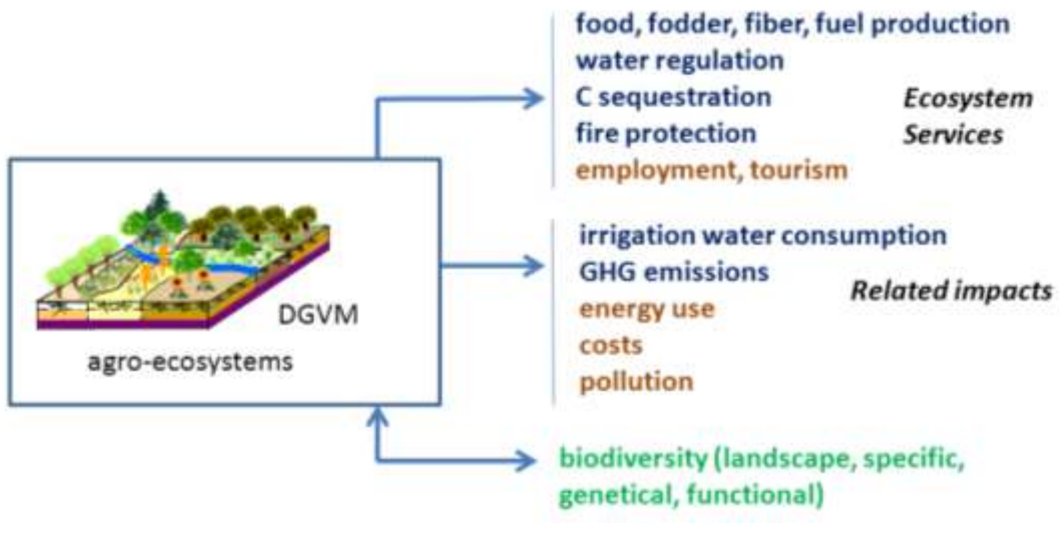

Figure 10 shows the ecosystem services and related impacts that can be directly simulated by LPJmL (in blue). The combination with data from other sources for other variables (in brown) will allow a broader-spectrum trade-off analysis, especially under different management scenarios and climate change.

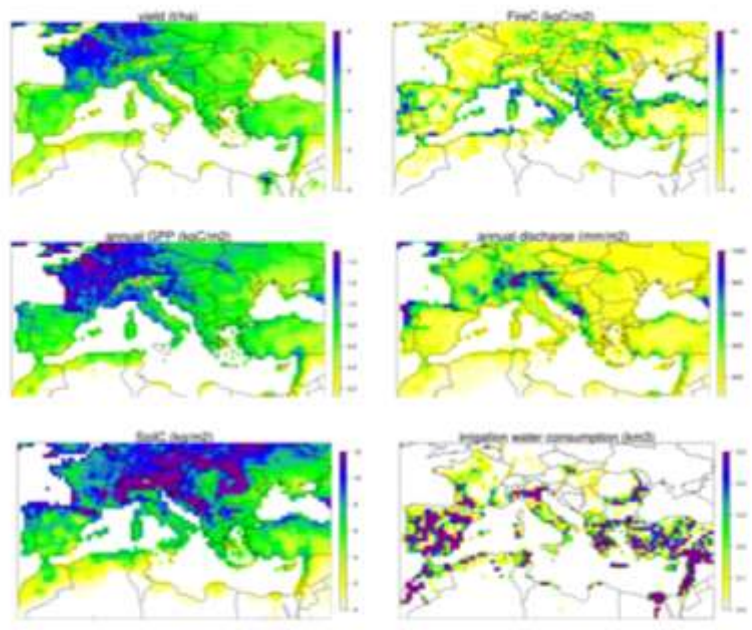

Figure 11 - Examples of LPJmL outputs for the Mediterranean exemplar.

The soil water assessment tool (**SWAT**) is a physically-based, conceptual, continuous-time river basin model with spatially semi-distributed parameters operating on a daily time step. It was designed to simulate broader scale patterns of discharge and water quality in the spatial and temporal domain (Neitsch *et al.*, 2005). The SWAT model integrates all relevant processes including water flow, nutrient transport and turnover, vegetation growth, land use, and water management at the sub-basin scale. It considers five different pools of nitrogen in the soils (Neitsch *et al.*, 2005): two inorganic (ammonium and nitrate) and three organic (fresh organic nitrogen and active and stable organic nitrogen). Nitrogen is added to the soil by fertilizer, manure or residue application, fixation by bacteria, and atmospheric deposition. Nitrogen losses occur by plant uptake, leaching, volatilization, denitrification and erosion. SWAT is a semi-distributed model: processes are simulated at hydrological response units (HRU). The HRUs contain similar terrain, similar soil characteristics, and similar land use and are assumed to respond similarly to management actions and climatic conditions. The water balance for each HRU is represented by four storages: snow, soil profile (up to ten layers), shallow aquifer, and deep aquifer. Soil water processes include evaporation, surface runoff, infiltration, plant uptake, lateral flow, and percolation to lower layers. The surface runoff from daily rainfall is estimated with a modification of the SCS curve number method (Arnold & Allen, 1996, Neitsch *et al.*, 2005). The different runoff components and matter fluxes are routed to the sub-basin outlets, where modeled and observed discharge as well as water quality data can be compared. In a current review of tools for estimating freshwater hydrological ecosystem services, SWAT was recommended by (Vigerstol & Aukema, 2011), given that data availability is adequate and that the user is qualified to use the model. (Lautenbach *et al.*, 2012a) used the Soil Water Assessment Tool (SWAT) to quantify and map water purification services by comparing water quality results with and without purification services provided by soils. (Lautenbach *et al.*, 2013) used the model to describe trade-offs between food and fodder provisioning, biofuel provisioning, water quality regulation and discharge regulation. (Logsdon & Chaubey, 2013) used the model to assess fresh water provisioning, fuel provisioning, erosion regulation and flood regulation.

Forest dynamic models have also been used for the assessment of bundles of ecosystem services including timber production, natural hazard regulation (avalanches and also rockfalls), carbon sequestration, conservation of forest diversity for greater drought resilience and habitat for protected bird species (Elkin *et al.*, 2013, Grêt-Regamey *et al.*, 2008, Temperli *et al.*, 2012).

More generally, process models have been applied for the assessment of the supply of a variety of regulation services. (Stürck *et al.*, 2014) quantified the supply of flood control by running a hydrological model for a number of representative catchment types to quantify the regulating effect of different land use types in different positions in the catchments. Results were extrapolated on a European map accounting for catchment type, location in the catchment, land use and soil conditions.

A model for the long-term carbon sequestration expected from seagrass restoration programmes was developed by (Duarte *et al.*, 2013) by combining models of patch growth, patch survival in seagrass planting projects and estimates of seagrass CO_2 sequestration per unit area for the five seagrass species commonly used in restoration programmes. Results indicated that the cumulative C sequestered increased rapidly over time and identified an optimal planting density to maximise C sequestration per planting effort at a density of 100 units ha^{-1}. At this density, the modelled cumulative C sequestered ranged from 177 to over 1337 tons CO_2 ha^{-1} after 50 years.

2.6.5.1. Example Application

Historical and future quantification of global Carbon Sequestration [1]

The functioning of ecosystems evolves in response to environmental drivers, such as climate, atmospheric carbon dioxide concentrations and land use which result from demographic and economic pressures on the Earth's biosphere (MEA, 2005). One ecosystem service that is particularly relevant on a global scale and strongly modified by human-induced environmental changes is the ability of the biosphere to either sequester or emit greenhouse gases (GHG). It can be quantified based on different indicators, such as organic matter storage (e.g. REDD+; (UNFCC, 2008)), flux of GHG to or from the atmosphere (e.g. (CCX, 2009)), or a combination of both (e.g. (IPCC, 2006)). However, each of these methods neglects one or more parts of the system, and thus is not accounting for all of the contributors of an ecosystem to regional and global climate that occur over a multi-

[1] Bayer, A.D., Arneth, A., Pugh, T.A.M.: Historical and future quantification of the carbon sequestration. In preparation.

year time span. An appropriate metric to value the full implications of biological carbon sequestration is provided with the recently introduced concept of the Greenhouse Gas Value (GHGV, (Anderson-Teixeira & De Lucia, 2011)). It is a suitable metric for this as it considers the contribution of multiple greenhouse gases to an ecosystem's effect on climate with accounting for their amount stored in an ecosystem, their annual flux and probable effects of natural disturbance. GHGV has the potential to become meaningful to policy makers as it comes in a unit that can be directly transferred into market values.

We adopted the concept of GHGV that is determined for CO2 to quantify carbon sequestration on global scale (0.5°x0.5° grid) using the LPJ-GUESS dynamic global vegetation model (Sitch *et al.*, 2003, Smith *et al.*, 2001). Quantification of GHGV by using a process-based modeling framework offers advantages as it introduces a time perspective to the metric, offers a consistent representation of ecosystem disturbance and allows for the direct attribution of changes in GHGV to changes in the environmental drivers climate, atmospheric CO2 concentration and land-use. LPJ-GUESS is run under different configurations, simulating (1) the potential natural vegetation that grows without human intervention, (2) considering C-N interaction for natural vegetation (Smith *et al.*, 2014) and (3) with a detailed representation of croplands and land-use change (Lindeskog *et al.*, 2013). Ecosystem state variables simulated for historical time periods (1850-2000) and future scenarios (2000-2100) are used to quantify the individual terms of GHGV in steps of 50 years. Ecosystem carbon storage is determined by a fire clearing the ecosystem and determining the CO2 that is released immediately from the combustion of aboveground biomass and from the decomposition of soil carbon stocks over 50 years. Contribution of carbon flux is included with the Net Ecosystem Exchange over 50 years. The contribution from natural disturbance to GHGV is directly included in these two terms when determined using the LPJ-GUESS model. GHGV provision of global ecosystems is evaluated on a biome basis because of the regionally disparate behavior of the terrestrial biosphere.

GHGV is simulated highest in the forest biomes, and especially tropical forests (Figure 12) following the large carbon storage and sequestration potential in these biomes. The forest biomes show a large intra-biome variability that is driven by the large temperature gradients. For the non-forest biomes, below 250 Mg CO2-eq ha-1 are simulated. Of these, the tundra biome is highest because of its significant carbon stocks in soils. GHGV significantly varies depending on the biogeochemical processes represented in LPJ-GUESS (e.g., C-N coupling, land-use). For instance, GHGV of ecosystems under current land use (approximated by year 2000) have about 19 % lower GHGV than is simulated for the ecosystems in their natural state. In addition, the representation of natural disturbance, which is explicitly represented in the LPJ-GUESS model, emerges as a major factor in GHGV quantification. In selected biomes (e.g. tropical savannas, temperate shrub/woodlands, tropical forests) the inclusion of natural disturbance accounts for changes in GHGV of up to 90 %.

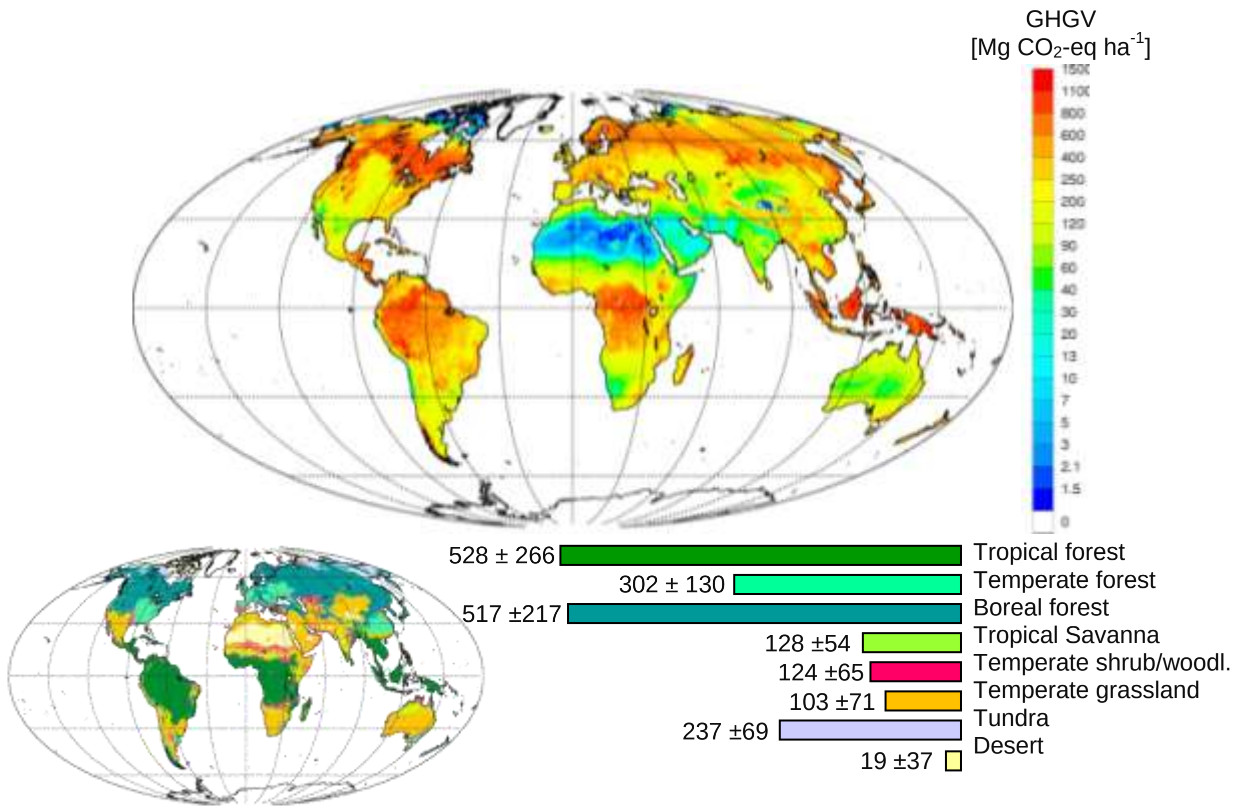

Figure 12 - Greenhouse Gas Value simulated for 2000 under consideration of actual land-use and management. Global average is 325 ± 267 Mg CO2-equivalents ha-1.

The influence of the three environmental drivers on ecosystem GHGV is evaluated by comparing a simulation set-up with all drivers variant with set-ups, where each one driver is fixed. The analysis projects a net negative impact of climatic changes on GHGV that is about -23 Mg CO2-eq ha-1 in 2000 on global average (Figure 13). It results of the positive effect of rising temperatures that promotes plant growth and efficiency in areas that were previously temperature limited being leveled off by the significant increase of soil respiration under rising temperatures which continuously releases CO2 that was so far stored in soils. Rising atmospheric CO2 concentration exerts a positive impact on GHGV due to the fertilization effect of CO2 on plant photosynthesis (**Erreur ! Source du renvoi introuvable.**), which is larger in low latitudes (Hickler et al. 2008). The effect of land-use is biome-specific (**Erreur ! Source du renvoi introuvable.**) and follows the historical transformation of natural vegetation into agricultural areas and the difference in carbon storage and carbon sequestration potential between these two systems.

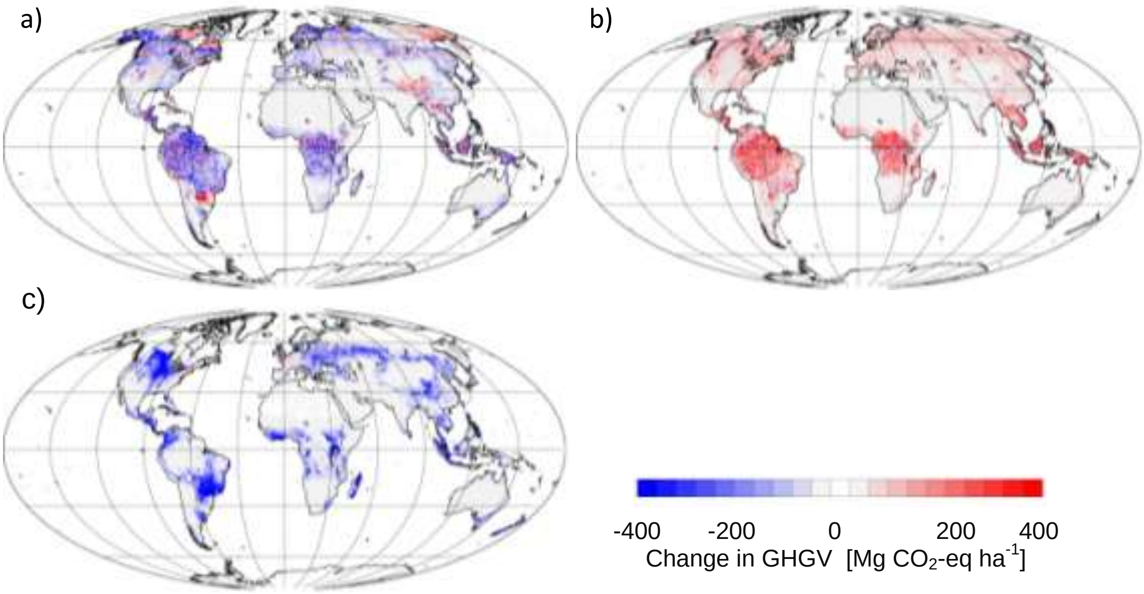

Figure 13 - Change in GHGV attributed to the environmental drivers climate (a), atmospheric CO2 concentration (b) and land use (c) alone from 1850 to 2000.

2.6.6. Data sources

Process models require high-quality data on a large scale. Various sources exist for observation-based climate forcing on different resolution with CRU TS 3.0 (Mitchell and Jones, 2005), GPCC (Rudolf *et al.*, 2010), WATCH Forcing Data (Weedon *et al.*, 2011) and ERA-Interim (ECMWF). A suite of climate models that can be used solely or in combination with observation-based climate is offered by the CMIP5 project (coupled-model inter-comparison project phase 5). Atmospheric CO2 concentration is available from the Mauna Loa series for different RCPs (Keeling et al., 2009). Historical land-use data are provided by, e.g., Hurtt et al. (2011) and Fader et al., (2010) which are derived from the combination of the MIRCA 2000 dataset (Portmann *et al.*, 2010) and cropland and pasture fractions following (Ramankutty *et al.*, 2008). Highly generalized classes of soil texture as used by process-based models are provided by the Harmonized World Soil Database (FAO/IIASA/ISRIC/ISSCAS/JRC, 2012).

2.6.7. Strengths and weaknesses for practice

There is a substantially overlapping set of physiological and ecological principles that is used by the existing process-based models to represent ecosystem dynamics and matter flows. However, predictions of response variables, e.g. net primary productivity, vary considerably among the models (e.g., (Denman *et al.*, 2007, Friedlingstein *et al.*, 2006, Sitch *et al.*, 2013)). These discrepancies are the result of the lack of a universal set of benchmarks e.g. for terrestrial carbon cycle modelling, and the lack of consensus about several aspects of ecological processes (Prentice & Cowling, 2013).

Typically process-based models need a lot of expertise to set them up and to produce reliable results. Model calibration against data is needed to apply most process-based models to the specific situation in a case study. Quite often process models have not been designed to model ecosystem services but to model the underlying ecosystem function from which an ecosystem service has to be derived. The great strength of this approach is that it allows scenario analysis and if-then-else experiments if the model has been proven to capture the essential system behaviour.

2.7. Discussion

Main biodiversity attributes and the strengths and weaknesses of different model types for practice are summarised in

Table 2.

Table 3 summarises the planned used of different types of models for a selection of OPERAs Examplars and illustrates: (1) the predominant effect of scale on model selection, (2) the ability within a single case study to combine different model types, of varying complexity and detail in the representation of biodiversity effects, depending on specific ES of interest, skills and data / resources availability.

Our categories are not necessarily exclusive and there may be more of a continuum between approaches. Hybridization is a fruitful avenue for model improvement depending on context, scale, skills and data availability. This is illustrated by a number of published examples and ongoing developments that gradually help progressing from MAES Tier 2 to Tier 3, by gradually incorporating more mechanistic approaches, and especially a greater integration of explicit biodiversity effect into mapping of ES supply. For instance, (Grêt-Regamey *et al.*, 2008) demonstrated how statistical, phenomenological and process-based models of varying level of complexity can be coupled with a GIS platform in order to assess ecosystem services at landscape scale. (Schirpke *et al.*, 2013) coupled the USLE process model of soil erosion with a semi-mechanistic statistical model of plant root trait effects on soil retention to quantify effects of land use change on soil stability. (Stürck *et al.*, 2014) used a hybridization between process-based models and spatial proxy models to optimally map flood regulation across the whole of Europe. This model determines flood regulation supply a process-based hydrological model to determine the regulating capacity of different land use-soil combinations in relations to the location within the catchment and thus construct a lookup table to extrapolate these relations to other catchments to avoid lengthy simulation procedures by running models for each individual catchment. Process-based DGVMs have also recently evolved towards the integration of trait-based approaches rather than using a small number of fixed Plant Functional Types. First, global vegetation models can be reformulated to incorporate plant traits and their trade-offs as drivers of vegetation distribution (Reu *et al.*, 2011). Second, recently developed DGVMs have started considering direct trait-based formulation (Scheiter & Higgins, 2009, Zaehle & Friend, 2010) and/or parameterisation (Verheijen *et al.*, 2013, Wullschleger *et al.*, 2014). Lastly, for landscape to regional scales so-called ‘hybrid’ DVMs pave the way to the integration of macroecological models with dispersal models (Midgley *et al.*, 2010) and with trait-based process models (Boulangeat *et al.*, 2012), thereby opening new perspectives for the refinement of the trait-based modelling of ES supply under scenarios of climate change (Boulangeat *et al.*, 2014). Together, all these recent developments illustrate how increasing fundamental understanding on the role of different facets of biodiversity for ecosystem functioning and ecosystem services (Cardinale *et al.*, 2012) can be incorporated into the spatially explicit modelling of ecosystem service supply.

Model type	Biodiversity representation	MAES Tier	Scales	Skill needs	Data needs	Evaluation	Transferability in space and time
Proxy-based	Absent (land cover / use) or basic (vegetation)	1	All	Low Tools: GIS application	Low-medium But potential lack of data layers (e.g. soils)	Rare	Large uncertainty if local or past / future conditions exceed those of model development (and validation)
Phenomenological	Basic or landscape processes	2	Mainly Local-regional	Low Tools: GIS application	Low-medium Maps or proxy of landscape elements. Other proxys (e.g. soils) dependent on availability.	Rare	Large uncertainty if local or past / future conditions exceed those of model development (and validation)
Macroecological	Species geographic distributions	2-3	Regional - continental	Medium Available tools : Maxent, BIOMOD	Medium Constrained by availability of modelled species distribution or of species distribution data.	Well developed	Designed for scenario projections Current limitations: lack of demographic and evolutionary processes
Trait-based	Trait effects on ecosystem functioning, and possibly spatial trait distributions	3	Local - regional	Medium-High Lack of readily available (or validated) models	Medium-High Constrained by availability of trait data and environmental layers (e.g. soils) Promise: remote-sensing of traits and soils	Easy but requires local data collection	Well-adapted for scenario projections. Risk of exceeding conditions / parameter space of model development
Process-based	Plant Functional Types Also possibly : individual species, traits	3	Landscape – continental - global	High Tools : Complex computer models	High High temporal resolution climate data, information on land cover change and N input	Well developed	Designed for scenario projections

Table 2 - Strengths and weaknesses of different model types for practice.

	SWISS ALPS	FRENCH ALPS	MONTADO	BALEARIC ISLANDS	SCOTLAND	MEDITERRANEAN	PAN EUROPEAN	GLOBAL
SPATIAL PROXY-BASED	Gene pool protection/biodiv. crop production, fodder production, carbon regulation, landscape aesthetics	Crop production, timber and fuelwood production, fodder production, C stocks, recreation	Crop production, livestock production, wild foods, fibres and materials from plants and animals, C sequestration, water flow maintenance, pollination	Carbon sequestration, carbon stocks, nutrient retention			Food crop production, Forest biomass stock, Potable water supply, Air quality regulation, Storm protection, Soil quality regulation	
PHENOMENO-LOGICAL		Pollination, erosion control		Carbon sequestration, nutrient retention	Pollination, flood control, erosion control, biocontrol		Carbon sequestration, Erosion prevention, Pollination, Recreation capacity	
MACRO-ECOLOGICAL		Biocontrol				Biocontrol(?), fire control(?)		
TRAIT-BASED	Fodder production (quantity, quality), soil fertility, plant diversity	Fodder production (quantity, quality), soil fertility [zoom]		Carbon sequestration, nutrient retention sediment retention and accumulation				
PROCESS-BASED	Natural hazard protection, timber production	Timber and fuelwood production (zoom), rockfall protection, water quality			Carbon sequestration, food production, fodder production, water supply, transpiration, timber(?), energy crops(?), soil fertility(?)	Carbon sequestration, food production, fodder production, bioenergy production, timber production(?), water flows regulation, climate regulation, water	Flood control	Carbon sequestration, food production, fodder production, water supply, transpiration, timber(?), energy crops(?), soil fertility(?)

Table 3 – Current model choices according to model types for a selection of OPERAs Examplars.

2.8. Data sources for improving the representation of biodiversity in spatially-explicit ES models

The second MAES report (Maes *et al.*, 2014) presents data sources at European scale for ES indicators. Here, we focus on specific aspects relating to parameterisation of biodiversity components in ES models.

2.8.1. Biodiversity data

Of potential use to ES mapping, and especially spatial proxy models, a European Landscape Map (LANMAP) has been produced, using landscape classification of Pan-Europe with four hierarchical levels; using digital data on climate, altitude, parent material and land use as determinant factors. This results in 350 landscape types at the most detailed level. At this level there are 14,000 mapping units across Europe with a minimum mapping unit of 11 km2 (Mücher *et al.*, 2010).

2.8.1.1. Vegetation data

Provide standardised vegetation description across geographic areas (Chytrý *et al.*, 2011). Across Europe, while there is a strong tradition in mapping vegetation, efforts are still underway to develop national data bases (available in some countries but not all) and a pan-European data base. The European Vegetation Archive (EVA) is an initiative of the European Vegetation Survey aimed at establishing and maintenance of a single data repository of vegetation-plot observations (i.e. records of plant taxon co-occurrence at particular sites, also called phytosociological relevés) from Europe and adjacent areas and to facilitate the use of these data for non-commercial purposes, mainly academic research and applications in nature conservation and ecological restoration (http://euroveg.org/eva-database). The Global Index of Vegetation-Plot Databases (GIVD; http://www.givd.info), is an Internet resource aimed at registering metadata on existing vegetation databases, most of which are currently located in Europe (Dengler *et al.*, 2011).

2.8.1.2. Species distribution data in Europe

In Europe occurrence data for all terrestrial vertebrate species have been collated for 187 mammals (Mitchell-Jones *et al.*, 1999), 445 breeding birds (Hagemeijer *et al.*, 1997), and 149 amphibians and reptiles (Gasc, 2004). (Maiorano *et al.*, 2013) further refined this data to model the spatial distribution of 275 mammals, 429 birds and 102 amphibians across the Palearctic at 300 m resolution by incorporating to each of the 46 GlobCover land use/land cover classes. A clustering at 10’ was further performed by (Zupan *et al.*, 2014). So far, extensive distribution data are only available for 1280 higher plants as part of the digitized Atlas Flora Europeae. For trees exhaustive data are available at a 1 km² resolution (http://www.efi.int/portal/virtual_library/information_services/mapping_services/tree_species_maps_for_european_forests/). More comprehensive species distribution data are available on a country per country basis, and also vary across regions within a same country.

2.8.1.3. Phylogenetic data

Overall, the availability of phylogenies is currently increasing, especially in Europe. Mega-phylogenies for higher plants, mammals and birds have been developed for Europe by (Thuiller *et al.*, 2011), further complemented for the Palearctic and amphibians by (Zupan *et al.*, 2014).

2.8.1.4. Functional trait data

Plant functional trait data are becoming increasingly available through the collation, curation and distribution of communal data bases (Kattge *et al.*, 2011). In general, more easily measurable traits such as plant size (e.g. vegetative height), leaf size, structural (e.g. Specific Leaf Area, Leaf Dry Matter Content) or chemical (e.g. C, N, P) concentrations, wood density or seed size have been measured for many species globally, and can also be measured on-site following standard methods (Cornelissen *et al.*, 2003). In contrast to this, traits requiring more time-consuming, expensive, or technically-demanding measurements, and especially root traits are poorly available. There are also definite geographic gaps, but overall European vegetation tends to be increasingly well covered, although more extreme environments such as Mediterranean or alpine, where intraspecific variability hinders the use of data measured in more temperate regions, still require collection efforts.

Trait data bases have also emerged for other biota such as birds (Pearman *et al.*, 2014), mammals (PanTHERIA (Jones *et al.*, 2009)), amphibians (http://amphibiaweb.org/), fish (FishBase (Froese & Pauly)), phytoplankton (Litchman & Klausmeier, 2008), lotic invertebrates (Survey), or soil invertebrates (e.g. (Salmon *et al.*, 2014) for Collembola). Such increasing trait data availability offers high promises for the development of trait-based models of ecosystem services.

2.8.2. Remote sensing for parameterizing ecosystem service models

Remote sensing can be defined as "the art and science of acquiring information about an object without being in direct physical contact with the object" (Jensen, 2007). Remote sensing information consists in measurements of the electromagnetic radiation of surface properties (sometimes ground or first centimeters of underground using active sensors like RADAR or LiDAR) using active or passive sensors. Interactions between incident radiation and surface elements are extremely complex and are described by three main physical mechanisms: absorption, reflection, and transmission.

Remote sensing is now commonly used in the fields of ecology, biodiversity and conservation (Wang *et al.*, 2010) and the potential for synergies between these fields of interest has been highlighted by many since the years 2000 (Pettorelli *et al.*, 2014). Remote sensing can provide consistent long-term Earth observation data from local to global scales. Compared with field-based observations, remote sensing is less labour-intensive and time consuming. Hence, remote sensing is increasingly used to quantify and map biodiversity, ecosystem functioning and ecosystem services (Ayanu et al., 2012, (Wang *et al.*, 2010), Turner et al., 2003, Nagendra 2001).

Remote sensing offers instantaneous spatially contiguous information, covers larger areas and in the case of satellite observations benefits from their revisit capacity. Therefore, remote sensing offers potential to complement or even replace field measurements of some key parameters for ES models such as soil parameters, vegetation composition or plant traits (Kokaly et al., 2009). Using remote sensing for studying ecological, biodiversity or conservation issues need effective collaborations between experts of the both fields (biology, ecology, geography, engineering), that have a large degree of overlap as abiotic environmental condition issues (Aplin, 2005, Pettorelli *et al.*, 2014, Turner *et al.*, 2003). Moreover the use of remotely sensed earth observation data is often constrained by access to data and processing capacity (Wang *et al.*, 2010).

Remote sensing is commonly used in vegetation mapping, where reflectance of vegetation canopies depends on radiative properties of leaves, other non-photosynthetic canopy elements and their spatial organization. Leaf reflectance spectra are mainly characterized by (i) strong and well described absorption of foliar photosynthetic pigments, dominated by chlorophylls, in the visible region (400–700 nm, VIS), (ii) leaf structure in the near infrared region (700–1300 nm, NIR), and (iii) prevailing water and protein absorptions (as well as other biochemicals) in the shortwave infrared region (1300–2500 nm, SWIR). The key factor influencing canopy reflectance is canopy structure (Disney *et al.*, 2006, Rautiainen *et al.*, 2004). The most widely used descriptor of canopy structure in RS studies is the leaf area index (LAI) (Fernandes *et al.*, 2004, Turner *et al.*, 1999).

While the potential of remote sensing data for mapping ecosystem services is large, practice indicates that successful integration of remote sensing observations and ecological applications still requires bridging gaps in scientific terminology (Schaepman-Strub *et al.*, 2006, Violle *et al.*, 2007) and scaling across leaf, plant and canopy levels (Malenovský *et al.*, 2007, Messier *et al.*, 2010). Below we summarise the main sources of remotely-sensed data that can be considered as promising sources for the mapping of ecosystem service supply (Homolová *et al.*, 2013). We end with an example of a first study comparing trait-based and remote sensing based models of ecosystem services for mountain grasslands of the French Alps (Homolová *et al.*, 2014).

2.8.2.1. Examples of significant traits for ecosystem service modelling and associated remote sensing methods

Table 4 summurises critical plant traits relevant to ecosystem functioning (Cornelissen *et al.*, 2003, Lavorel & Garnier, 2002) and thus modelling of ecosystem service supply, and their possible remote sensing counterparts.

Plant height is an important trait associated with plant competitive abilities, and has been shown to be relevant to provisioning (fodder and timber supply) or regulation (e.g. climate regulation through carbon sequestration) services (Lavorel, 2013). Laser scanning has emerged to be the most accurate remote sensing technology for the measurement of plant and canopy height. The best absolute accuracies achieved in tree height estimation are produced from airborne discrete return laser scanners (LiDAR). It faces three major issues: 1- the determination of the terrain elevation, which is difficult in very low or too dense canopies, where emitted signal cannot penetrate to the ground (Falkowski et al., 2008; Lefsky, 2002) ; 2- the accurate detection of the uppermost canopy layer, which depends on the sampling pulse density (Jakubowski et al., 2013; Magnusson et al., 2007) ; 3- height accuracy decreases with decreasing sampling pulse density, but remains relatively constant and high until the densities drops below 1 pulse/m2 (Jakubowski et al., 2013).

Phenology (seasonal timing) is closely related to plant nutrition conservation and competitive strategies and is influenced by local meteorological, topographic and soil variations (Dahlgren et al., 2007). In grasslands for example, phenology contributes to the temporal component of fodder production through the farming season, or to aesthetic value (Lavorel *et al.*, 2011). For plant communities that periodically change their foliar apparatus, time series of remote sensing data provide an effective means of extracting land surface phenology (LSP) indicators including start, end, duration and maximum peak of the vegetation season (Liang and Schwartz, 2009; Reed et al., 1994). Typical temporal and spatial resolutions of remote sensing data used for LSP analysis are biweekly composites of vegetation indices of global spatial extent and a pixel size ranging from 0.25 to 8 km (e.g. MODIS (Huete et al., 2002), AVHRR NDVI time series (Tucker et al., 2005)). The estimation of the LSP indicators from the satellite RS is influenced by four factors: (i) temporal resolution (Kross et al., 2011), (ii) missing or noisy data due to clouds or snow cover (Delbart et al., 2006), (iii) magnitude of the seasonal amplitude in vegetation greenness to override other sources of variation (e.g. earlier greening of understory), and (iv) a method extracting the phenology indicators (de Beurs and Henebry, 2010; White et al., 2009).

Leaf dry matter content (LDMC in mg g^{-1}) and **specific leaf area** (SLA in m^2 g^{-1}) are two traits with close functional links. LDMC negatively correlates with SLA (Garnier et al., 2001; Shipley and Vu, 2002; Vile et al., 2005) and both traits are related to plant growth rate and leaf resistance to physical damage. As such they contribute to biomass production and hence to provisioning services, as well as to both the quality of plant material for wild or domestic herbivores (Gardarin *et al.*, 2014, Ibanez *et al.*, 2013), and, through litter decomposability (Cornwell *et al.*, 2008, Fortunel *et al.*, 2009), to carbon and nutrient recycling and hence both C sequestration and the maintenance of soil fertility. It is important to note first that some RS studies use terms ‘‘leaf dry matter content’’ or ‘‘dry matter content’’ when actually referring to leaf mass per area (LMA) – the inverse ratio of SLA (Riano et al., 2005; Schaepman et al., 2004; Vohland et al., 2010). LMA can be retrieved from RS data using empirical, as well as physical methods, because LMA is an input into leaf RTM (Jacquemoud et al., 2009). Despite this fact, only a few RS studies specifically targeted LMA estimation from proximal or remote sensing data achieving rather inconsistent results. SWIR wavelengths are most important for LMA estimation (Asner et al., 2011; Kokaly et al., 2009), but they are also strongly influenced by water absorption (Rian˜o et al., 2005).

Nitrogen (N) is an important component in proteins, nucleic acids and chlorophylls and therefore strongly linked to plant photosynthesis (Reich et al., 1995) and gross primary productivity (LeBauer and Treseder, 2008; Smith et al., 2002). Like SLA and LDMC to which it is respectively positively and negatively correlated, leaf Nitrogen concentration has been repeatedly selected in models of provisioning and regulation services as a result of its contribution to biomass production, its quality to domestic and wild herbivores and its important role for carbon and nutrient recycling including through soil food webs (Lavorel, 2013). Currently the best way to estimate N from optical remote sensing is by means of empirical methods, because physically based retrievals are not well established. The only leaf RTM having N as an input is the LIBERTY model (Dawson et al., 1999). This model is not often used among the RS research community, which prefers using a simpler model– PROSPECT (Jacquemoud et al., 1996). Though there were attempts to incorporate N into PROSPECT, they were abandoned due to its strong covariance with other N containing compounds leading to inconsistent results (Jacquemoud et al., 1996; Kokaly et al., 2009). Among many empirical approaches, several VIs were proposed specifically to estimate leaf N and they were mainly established for crops (Chen et al., 2010; Tian et al., 2011). Also band selection techniques, such as stepwise or partial least square regressions, were successfully applied on transformed reflectance spectra (Smith et al., 2003; Yoder and Pettigrew-Crosby, 1995).

Leaf phosphorus (P) is an indicator of plant growth rate and nutrient quality, and has been implicated in some models of nutrient recycling. Only a limited number of studies have estimated Leaf P concentration from remote sensing data. Only Porder et al. (2005) used airborne remote sensing to estimate canopy P concentration of broadleaf tropical forest. The rest of the reviewed studies used airborne based or proximal sensing to estimate P concentration in structurally homogeneous canopies, such as crops and grasslands.

Plant traits from Cornelissen *et al.* (2003) [typical units]	Trait definition	Remote sensing methods	Operational scale: Leaf	Ind.	Pop./Com.	Ecosystem	Biome	LOSU
Plant/canopy height **[m]**	Distance between ground and the upper boundary of the main photosynthetic tissue	Directly derived from laser scanning data		*	*	*		4-5
		Indirectly related to Leaf Area Index (LAI)			*	*		2
Leaf phenology **[months]**	Number of month per year when canopy is green	For plant periodically changing leaves the length of the growing season is derived from satellite multi-temporal data				*	*	4
		Proximal phenological cameras		*	*			4
Specific leaf area **[m^2 kg^{-1}]**	One-sided area of a fresh leaf divided by its dry mass	Directly estimated as leaf mass per area (1/SLA) from RTM inversion			*	*		2-3
		Related to leaf water content that can be estimated from RTM inversion or empirical methods		*	*	*	*	3-4
Leaf dry matter content **[mg g^{-1}]**	Dry mass of leaf divided by its fresh mass	Empirical method estimating individual components such as lignin or cellulose		*	*	*		2
		Related to specific leaf area (see above)						
Leaf nitrogen concentration/content **[mg g^{-1} /mg m^{-2}]**		Directly estimated using empirical remote sensing methods		*	*	*		3
		Indirectly related to chlorophyll content that can be estimated using RTM inversion	*	*	*	*		4-5
Leaf phosphorus concentration/content **[mg g^{-1} /mg m^{-2}]**		Directly estimated using empirical remote sensing methods		*	*	*		2-3

LOSU (level of scientific understanding) indicates the fidelity of remote sensing methods and remote sensing based products used in vegetation studies. It represents a weighted average of scores for the number of reported studies and obtained accuracy of remote sensing methods (1 is low, 2 is low medium, 3 is medium, 4 is medium-high, and 5 is high level of the scientific understanding).

Table 4 - Link between plant traits relevant to ecosystem functioning (Lavorel & Garnier 2002, Cornelissen et al. 2003) and thus modelling of ecosystem service supply; and their possible remote sensing counterparts.

2.8.2.2. Matching remote sensing methods with ecological scales

Methods used to interpret optical RS data can be divided into two broad groups: empirical (statistical relationships between RS data and field trait observation) and physical methods (based on radiative transfer models -RTMs), or combination of both (Liang, 2004). Figure 14 summarizes an attempt to match scaling terminology used in ecology and RS (Homolová *et al.*, 2013), given the requirement for matching the spatial scales of trait with remote sensing data.

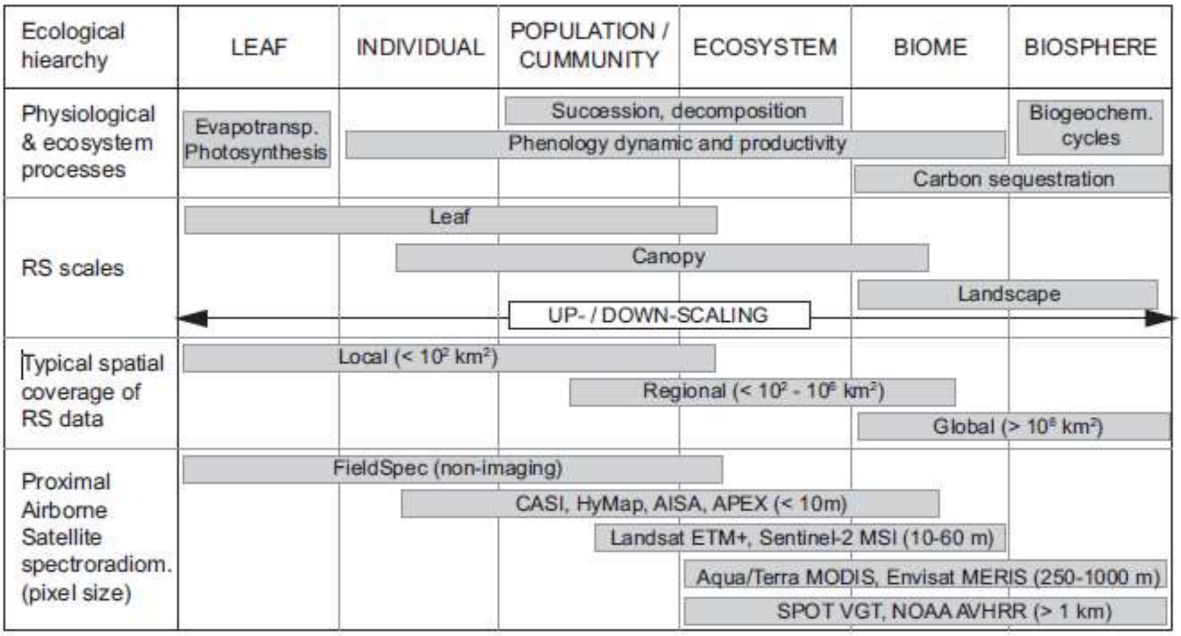

Figure 14 - Link between ecological and remote sensing spatial scales with examples of typical remote sensing spectroradiometers operational at variety of spatial scales.

For example, quantitative traits such as nitrogen are usually measured at the level of individual leaves of dominant plant species and expressed either as concentration (mass fraction per unit dry leaf mass) or content (mass fraction per unit leaf area) (here we refer to the terminology introduced by Datt (1998)). Based on the mass ratio hypothesis (Grime, 1998), leaf-level measurements can be further upscaled to the community (canopy) level by calculating a weighted mean using relative abundances of the most dominant species (Lavorel et al., 2008). This community weighted mean of a leaf trait is not directly comparable with RS, unless a physical scaling using leaf-canopy RTMs is applied to interpret RS data (Malenovsky´ et al., 2007). The product of community weighted mean with biomass or LAI, provides a canopy integrated value (i.e. canopy property) expressed per unit surface area (Table 4), which can be directly compatible with remotely sensed canopy reflectance. Ultimately, RS spectroradiometers measure a mixed signal reflected from entire plants (including woody and dry elements) and soil background. Information content originating from the green vegetation fraction can be enhanced by downscaling techniques – spectral unmixing or data fusion (Malenovsky´ et al., 2007). However, interpretation of RS data in areas with fractional vegetation cover below 30% remains extremely difficult (Okin et al., 2001) and largely non-conclusive. Therefore using different data sources, provided by field based-observation, very high spatial and spectral resolution sensors and 3D imagery (LiDAR), and data fusion techniques could produce the most detailed representation of vegetation cover and diversity, and so produce the best ES models.

2.8.2.3. Comparing remote sensing and plant trait-based modelling to predict ecosystem services in moutain grasslands (French Alps Examplar)

In this study, we used high spatial and spectral resolution RS images to assess multiple ES based on underpinning ecosystem properties (EP) of subalpine grasslands. We estimated five ecosystem properties (green biomass, litter mass, crude protein content, species diversity and soil carbon content) from remote sensing data using empirical RS methods and maps of ecosystem services were calculated as simple linear combinations of EP. Additionally, the RS-based results were compared with results of a plant trait-based statistical modelling approach that predicted EP and ES from land use, abiotic and plant trait data (modelling approach) (Figure 15). The comparison between the RS and the modelling approaches showed that RS-based results provided better insight into the fine-grained spatial distribution of EP and thereby ES, whereas the modelling approach reflected the land use signal that underpinned trait-based models of EP (

Figure 16). The spatial agreement between the two approaches at a 20 m resolution varied between 16 and 22% for individual EP, but for the total ecosystem service supply it was only 7%. Furthermore, the modelling approach identified the alpine grazed meadows land use class as areas with delivery of multiple ES (hot spots) and mown-grazed permanent meadows as areas of delivery of only few ES (cold spots). RS-based hot spots were a small subset of those predicted by the modelling approach. We conclude that despite limitations associated with the timing of assessment campaigns and field data requirements, RS offers valuable data for spatially continuous mapping of EP and can thus supply RS-based proxies of ES. Although the RS approach was applied to a limited area and for one type of ecosystem, we believe that the broader availability of high fidelity airborne and satellite RS data will promote RS-based assessment of ES to larger areas and other ecosystems.

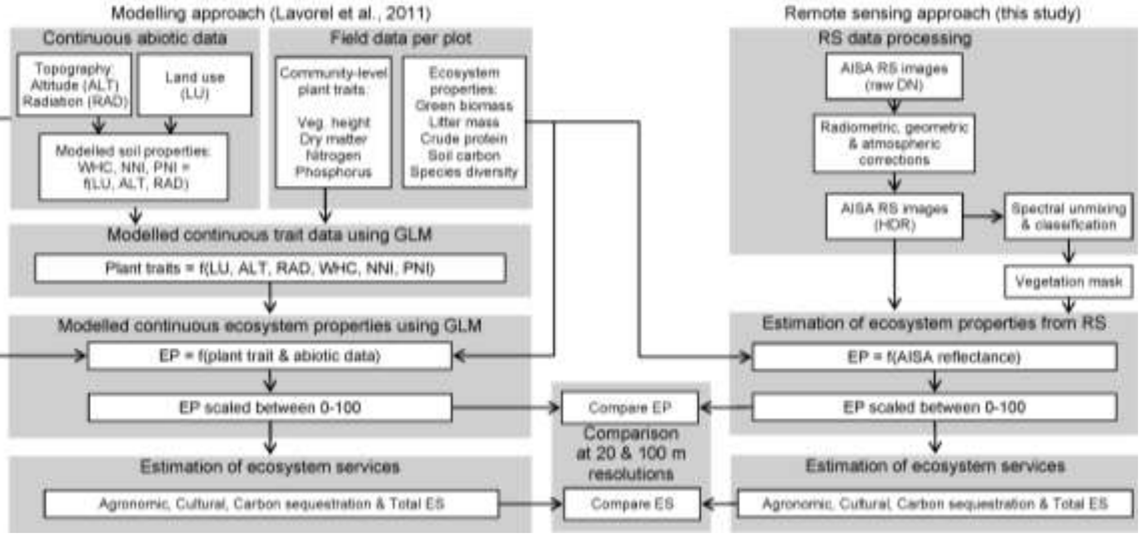

Figure 15 - Conceptual framework for the remote sensing of ecosystem properties and services and the comparison with the plant trait-based modelling approach. Abbreviations: water holding capacity (WHC), nitrogen nutrition index (NNI), phosphorus nutrition index (PNI), ecosystem properties (EP), ecosystem services (ES), remote sensing (RS), digital numbers (DN), hemispherical-directional reflectance (HDR).

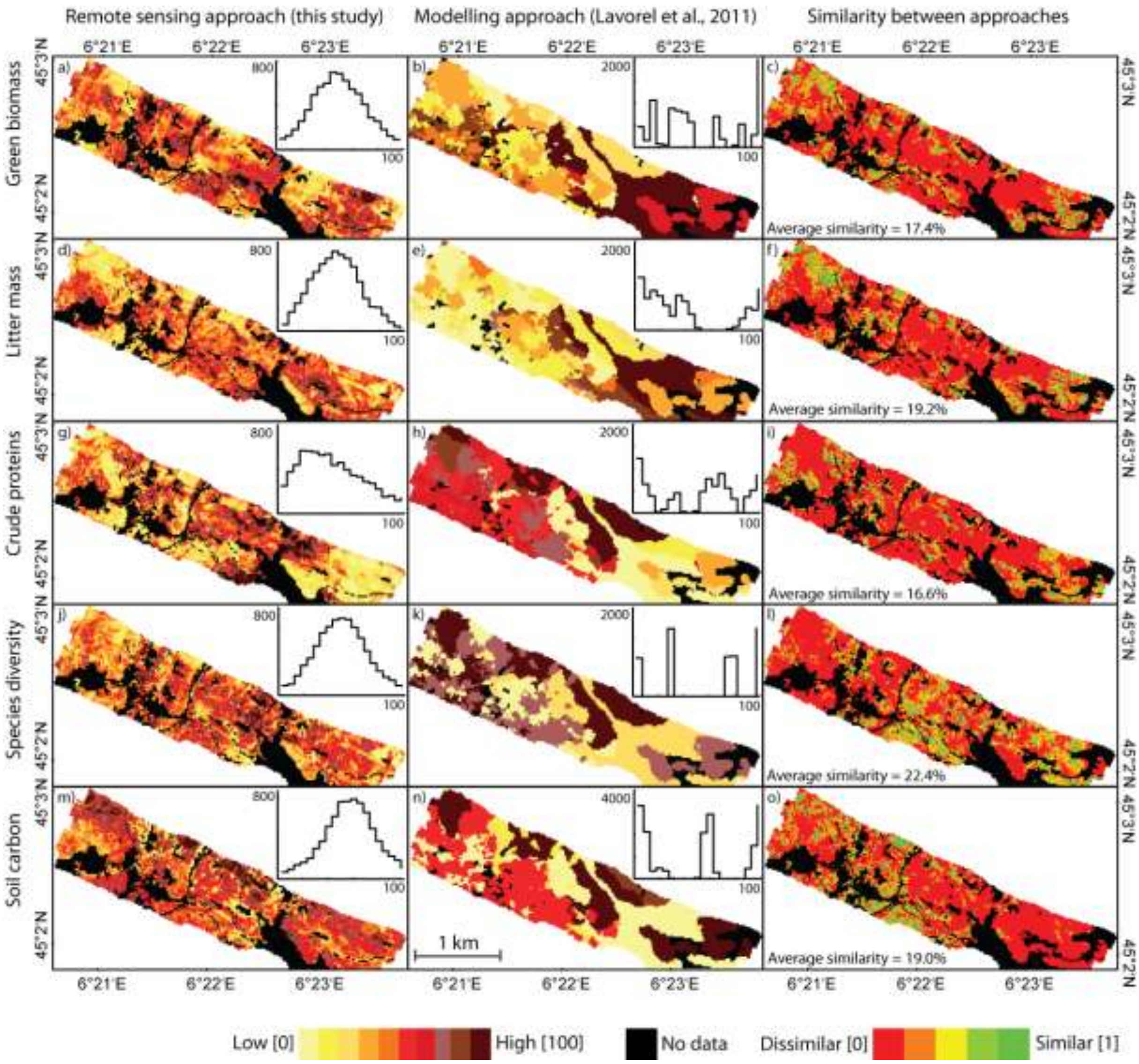

Figure 16 - Ecosystem properties estimated from the remote sensing approach and the modelling approach at a spatial resolution of 20 m. The most right maps show similarity between remote sensing and modelling approach. Frequency histograms show the distribution of values within the image.

3. Uncertainty and validation of spatially-explicit models of ES supply

Results from the OPERAs Milestone 2.3 meta-analysis showed that frequently ES models are neither validated nor are their uncertainties quantified. The two dimensions of good modelling practice are not independent of each other: case studies that consider uncertainty at least qualitatively have a significant higher chance of having validated the model or the results (Figure 17). For some ES categories, good modelling practices are applied more frequently than for others. P2 and P4 are validated significantly more frequently while C3 and C5 are validated less frequently (Figure 18 – see Table 1 for the list of services and their codes). For the categories C3 and S3 any kind of uncertainty analysis (quantitative or qualitative) is done significantly less frequently than on average, while case studies that did treat P4 are more frequently analyzed with respect to uncertainty (Figure 19). R3 and C2 are the ES categories in which both validation and a quantitative uncertainty analysis have taken place more frequently while R1 and C3 have significantly a lower percentage of studies that followed that good modelling practice. Cases studies that used lookup tables (i.e. proxy-based models) significantly less frequently validated their results. They also show a marginally significant chance of quantifying the attached uncertainty. An analysis of the detailed model types did not bring up any significant differences with respect to good modelling practice. While the total number of case studies that quantified uncertainty or validated the results have in the last increased in the last years, the relative numbers have not increased significantly.

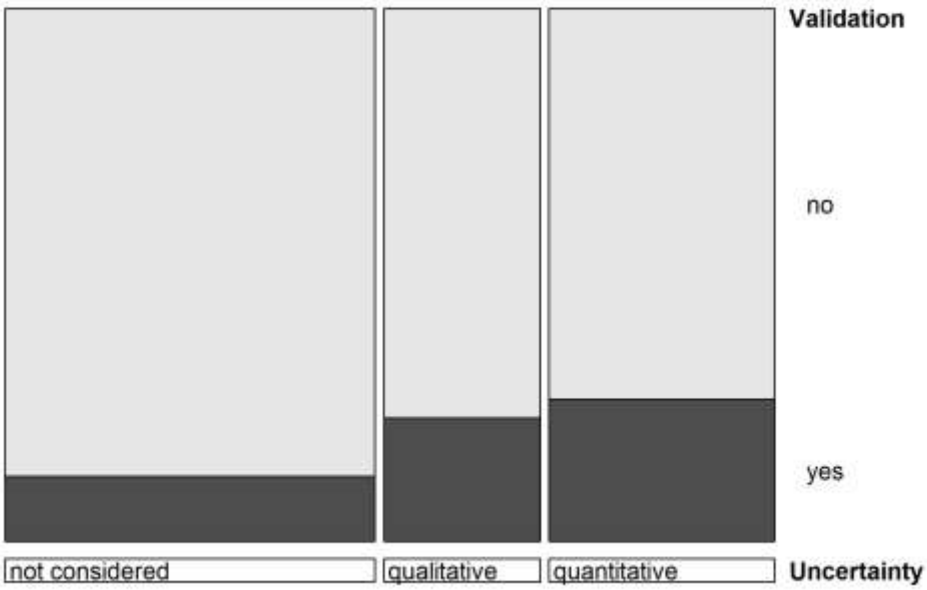

Figure 17 - Number of case studies that followed good modeling practice to validate the results and to investigate the attached uncertainty.

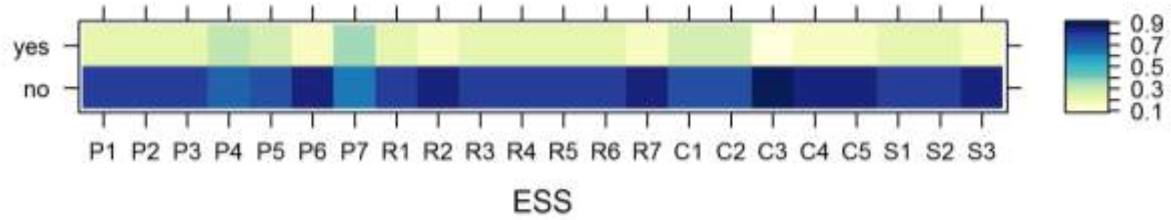

Figure 18. Number of case studies that validated the results by ES category. Values have been normalized by number of studies in each ES category. See Table 1 for the list of ecosystem services and their codes.

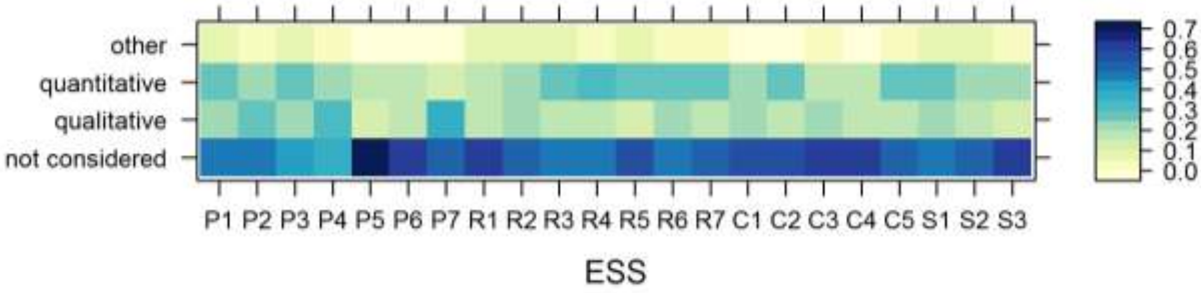

Figure 19. Number of case studies that considered uncertainty by ES category. Values have been normalized by number of studies in each ES category. See Table 1 for the list of ecosystem services and their codes.

(Hou *et al.*, 2013) provide an overview about how uncertainty analysis might be performed in the context of spatial explicit ES assessment and landscape analysis. They used the following groups of sources of uncertainty:

1. Uncertainty due to general systems principles
2. Uncertainty due to system analysis methods
3. Uncertainty due to ecosystem and landscape dynamics
4. Uncertainty due to modelling methodologies
5. Uncertainty due to landscape analytical methods
6. Uncertainty due to valuation methods
7. Uncertainty due to natural supply of services
8. Uncertainty due to preference settings
9. Uncertainty due to technical problems

Users should be aware of the different sources of uncertainty and at least list them with respect to their application. In addition to this qualitative step a quantitative assessment of the uncertainties of model output should be given. The different modelling approaches allow different levels of uncertainty assessments. If observed data is used it should be always possible to quantify deviates from measured data and to provide an estimate of the uncertainty attached. If no observed data is available against which model output could be compared sensitivity analysis is an option to quantify uncertainties based on model parameter uncertainty and uncertainty of model input data.

For species-distribution modelling see among others (Buisson *et al.*, 2009, Morin & Thuiller, 2009)

For phenomenological modelling approaches uncertainties can be assed based on a sensitivity analysis: by changing parameter values the sensitivity of the results toward model parameters can be assessed. Examples for this approach can be found in (Lautenbach *et al.*, 2011) and (Schulp *et al.*, 2014a). It is also possible to test the sensitivity towards the uncertainty in the input data, an approach followed in (Lautenbach *et al.*, 2012b).

For process-based models calibrated against data, uncertainties should be expressed at least by stating the model efficiency and the relative bias for the calibration and the validation period. Additional uncertainties occur if the calibration data is not well suited for the model outcome – e.g. it might be at the wrong temporal or spatial scale or measure or proxy instead of the modelled output.

3.1. Validation

The only way to estimate the reliability of any type of model is a test against independent data and an analysis of the uncertainty of the model predictions. While this is accepted knowledge in the environmental modelling community (Bennett *et al.*, 2012, Dormann *et al.*, 2008, Jakeman *et al.*, 2006, Laniak *et al.*, 2013), this has not been taken on by the majority of the ES community. The predominant lack of validation noted by (Crossman *et al.*, 2013a, Martinez-Harms & Balvanera, 2012, Seppelt *et al.*, 2011b) remains as a recurring gap in practice, as highlighted by Milestone 2.3.

Validation of models is complicated by the fact that data on ecosystem services are hard to get since a realized service is not as easy to measure as the underlying bio-physical structure. Therefore, model calibration as well as validation has to rely on proxy data quite frequently. Since these proxy variables are likely to be influenced by confounding factors model validation has to follow more a pattern oriented approach that tries to capture the system behaviour instead of or in addition to targeting observation data exactly. Water purification for example has to rely on water quality data not on measured purification rates – (Lautenbach *et al.*, 2012a).

3.2. A solution to validation and uncertainty analysis for spatial models of ecosystem services: Comparisons

In the absence of independent validation data and full-fledged uncertainty analysis a possible means to get insight into some of the uncertainties embedded in ecosystem service quantifications and maps is the comparison of existing maps. Within the context of OPERAs such an analysis was performed. The section below provides an overview of the results as reported in more detail in a recent paper submitted for publication[2].

Concerns were raised about the accuracy of ecosystem service maps and inconsistencies among mapping approaches (Eigenbrod *et al.*, 2010, Hou *et al.*, 2013). There is for example little knowledge about the influence of the mapping method and input data on the representation of spatial patterns of ecosystem service supply (Kandziora *et al.*, 2013). Most of the mapping studies pay little attention to uncertainties and error propagation (Hou *et al.*, 2013), and studies on ecosystem service map validation are lacking (Seppelt *et al.*, 2011b). Here, we identify uncertainties in continental-scale ecosystem service maps. Based on a systematic comparison of maps for the EU territory for five ecosystem services (climate regulation, flood regulation, erosion protection, pollination, and recreation), we map spatial patterns of agreement and disagreement for the provision of these five services. We evaluate sources of uncertainty and recommend best practices for ecosystem service mapping for policy support.

3.2.1. Methods

We analysed uncertainties in ecosystem service maps building on four consistent and published sets of ecosystem service maps at the EU scale (Table 5). First, (Burkhard *et al.*, 2012) map the capacity to provide ecosystem services at the European scale using an expert-based classification of land cover data (hereafter referred to as: LC approach). Second, (Kienast *et al.*, 2009)provide an expert-based map of landscape capacities to provide ecosystem services based on a broad set of environmental variables (EV approach). A third set of ecosystem service maps originate from a hybrid approach building on available data (Maes *et al.*, 2012) (JRC approach). The fourth set is also based on a hybrid approach but using different data and models (Schulp et al., 2008; 2014; Sturck et al., 2014; (Tucker *et al.*, 2013); van Berkel and Verburg, 2011) (IVM approach). Each set of maps contains estimates for climate regulation, flood regulation, pollination, erosion protection, and recreation. In addition to these four sets that all contain the same five ecosystem services, other studies are available that map one single ecosystem service (Table 5).

[2] *CJE Schulp, B Burkhard, J Maes, J van Vliet , PH Verburg. (in review). Uncertainties in ecosystem service maps: a comparison on the European scale*

Dataset	Climate regulation	Flood regulation	Pollination	Erosion protection	Recreation
Datasets included in full analysis					
LC approach[1]	Capacity of the landscape to provide the service. Based on categorical links between land cover and the service, using CORINE land cover data[2]. Categorical, 6 classes ranging from no capacity to very high capacity. 100m resolution.				
EV approach[3]	Capacity of the landscape to provide the service, expressed as an index based on a set of binary links between environmental variables (including CORINE land cover) and the ecosystem service. Continuous (Dimensionless). NUTS2 resolution.				
JRC approach	Carbon flow, expressed as Net Ecosystem Productivity (NEP). Based on a model based on RS image interpretation[4].	Water quantity regulation: Annually aggregated soil infiltration, derived from a pollutant pathway model. $1km^2$ resolution[4].	Visitation probability, based on distance decay function from pollinator habitat, multiplied with dependency level of pollinator dependent crops. Based on a crop type map and CORINE land cover. $1km^2$ resolution[5].	Area based indicator to express the protective function of forests and semi-natural areas based on CORINE land cover in areas with high erosion risk. $1km^2$ resolution[4].	Capacity of the landscape to provide recreational services. Dimensionless index based on the degree of naturalness, presence of protected areas, distance to coasts, lakes and rivers and bathing water quality. $1km^2$ resolution[4].
IVM approach	Carbon sequestration, expressed as NEP. Bookkeeping model where detailed flux measurements and simulations are aggregate to country-specific, land use type (based on aggregated CORINE land cover) specific emission factors. $1km^2$ resolution[6].	Index of flood regulation provision. Based on upscaling of catchment-scale simulations with a process-based hydrological model, to EU scale, using catchment characteristics like land use, topography and soil characteristics. $1km^2$ resolution[7].	Visitation probability, based on distance decay function from pollinator habitat. Based on CORINE land cover and a map of green linear elements[8].	Protection against erosion by vegetation, based on the Universal Soil Loss Equation and an aggregated version of CORINE land cover. $1km^2$ resolution[9].	Capacity of the landscape to provide recreational services. Dimensionless index, based on the degree of naturalness; presence of protected areas, presence of coasts, lakes and rivers, presence of High Nature Value farmlands[10].
Additional maps					
	Carbon storage: Coupling of global-scale carbon stocks to European-scale land use maps (CORINE land cover) 250m resolution.[11].	Natural hazard reduction: Influence of ecosystem structure on dampening environmental disturbances. Capacity of the landscape to provide the service, following EV approach[3].	Habitat percentage: Area percentage of pollinator habitat. Based on CORINE land cover and a map of green linear elements. $1km^2$ resolution[8].		
	Net Ecosystem Productivity (NEP) as calculated with the process-based LPJ model for the global carbon cycle. 0.5° resolution[12].		Habitat percentage: Pollinator habitat within a 2km range of croplands. $1km^2$ resolution[13].		

[1]: (Burkhard et al., 2012)
[2]: (EEA, 2000)
[3]: (Kienast et al., 2009)
[4]: (Maes et al., 2013a)
[5]: (Zulian et al., 2013)
[6]: (Schulp et al., 2008)
[7]: (Sturck et al., 2014)
[8]: (Schulp et al., 2014)
[9]: (Tucker et al., 2014)
[10]: (van Berkel and Verburg, 2011)
[11]: (Maes et al., 2011)
[12]: (Lehsten et al., in preparation)
[13]: (Serna-Chavez et al., 2014)

Table 5 - Overview of the ecosystem service datasets analysed in this study.

3.2.2. Map preparation

Available ecosystem services maps strongly differ in representation of the services, units, range of output values and spatial resolution (Table 5). Therefore, we aggregated and normalised all datasets to enable comparison. All maps were aggregated to NUTS2 regions[3] using the mean value for the ecosystem service for each region. This was done because the NUTS2 level represented the resolution of the least detailed map. All maps were subsequently normalised using a min-max normalisation to cover the range [0,1] with 0 indicating the lowest value for an ecosystem service. The LC maps are categorical maps where we assumed the categories to be linearly related following: no=0, very low=0.2, low=0.4, moderate=0.6, high=0.8, very high=1. For the EV maps, we assumed linearity in the values. To summarise maps of individual services, we calculated an ecosystem service bundle map for each of the four sets of maps (LC, EV, JRC, IVM). These bundle maps were defined as the sum of the five normalised ecosystem service maps. High values thus indicate locations with a relatively high supply or multiple services, while low values indicate the opposite. These bundle maps were included in the comparison because policies aim at protecting the overall level of ecosystem service provision rather than the provision of individual services (European Commission, 2011).

3.2.3. Map comparison and analysis

Maps for individual ecosystem services as well as the bundles were analysed both pair-wise and for all maps together. Pair-wise comparisons express the relative difference between two maps using Équation 1:

$$MCS = \frac{\sum_{n=1}^{N} \left(|a - b| / \max\left(|a|, |b|\right) \right)}{N}$$

Équation 1

Where MCS is the Map Comparison Statistic, *a* and *b* are the normalized values of an ecosystem service in a particular NUTS2 region, N is the number of NUTS2 regions considered. MCS values were computed for all available ecosystem services maps. This comparison statistic was chosen because it is symmetric (yielding the same result independent of which of the maps is map a or b), has a defined range (zero for two equal maps; one for two completely contrasting maps) (Hagen-Zanker, 2006).

To analyse the agreement in spatial patterns of ES in the four sets of maps (LC, EV, JRC, IVM), we calculated hotspot and coldspot maps. Hotspots and coldspots are areas providing, respectively, high and low amounts of a particular ecosystem service (García-Nieto *et al.*,

[3] NUTS is the EU Nomenclature of Territorial Units for Statistics; NUTS2 designates the basic regions for the application of regional policies.

2013, Gimona & Horst, 2007) and are defined as areas where the ecosystem service supply values fall within the upper or lower quartile of its value distribution. Agreement between the hotspot and coldspot maps of the four mapping approaches was calculated by counting the number of maps that indicated a hotspot or coldspot at a certain region. In addition, we calculated the mean value over the four included maps, as well as the coefficient of variation (CV); the standard deviation divided by mean. The mean over the four included maps gives an indication of the ES provisioning in each region, while the CV is an indicator for the uncertainty in the ES map. To support analysis of the sources of uncertainty, maps were compared with spatial patterns of land cover. We calculated correlations between the percentage of a specific land cover per region and the mapped provisioning of an ecosystem service.

3.2.4. Results

Differences among the climate regulation maps are modest with MCS values of 0.27 and lower (Table 6). However, when the four maps included in this study are compared to a process-based estimate (Lehsten et al., in preparation), larger differences are found, with MCS values up to 0.46 for the comparison with the LC map. A map of carbon stocks (Maes *et al.*, 2013b) (Table 5) compares reasonably with all other climate regulation maps; MCS values range between 0.13 (EV map) and 0.24 (LC map). The recreation maps also show modest differences between the maps. MCS values for pollination are higher and range up to 0.49 for the comparison between the JRC map and the IVM map. The maps were also compared to two other maps that are an indicator of the available potential pollinator habitat. The map by (Serna-Chavez *et al.*, 2014) is close to the LC map (MCS: 0.19) but deviates from the JRC map (MCS: 0.44). The habitat map by Schulp et al. (2014) is most similar to the JRC map (MCS: 0.19) and deviates most from the IVM map (MCS: 0.38). Flood regulation and erosion protection show high MCS values, indicating that the maps are more different from each other than maps for the other ecosystem services.

For the ecosystem service bundles, the MCS values are lower than for the individual service maps (Table 6). While for the individual services the JRC maps and IVM maps are most deviating, the bundle maps of JRC and IVM are the most similar, because differences amongst ecosystem services average out.

For *climate regulation,* there is agreement on the location of a coldspot in the Northwestern EU while there is reasonable agreement on hotspots in the Central Mediterranean region (Figure 20). These coldspots and hotspots can also be seen in the average climate regulation map (Figure 21). High climate regulation capacities are also found in Scandinavia because of the high percentage forest cover, but here the maps strongly disagree.

P*ollination maps* agree on hotspots in Southern Europe and coldspots in Western and Eastern Europe, while disagreement is seen in Central and Northern Europe (Figure 20). The areas where the maps disagree have a high level of pollination provisioning on average (Figure 21).

Map comparison	Service

	Climate	Flood regulation	Pollination	Erosion protection	Recreation	Bundle
LC-EV	*0.27*	0.28	0.23	0.26	0.28	0.18
LC-JRC	0.18	0.44	0.30	0.26	0.25	0.14
LC-IVM	0.27	0.17	0.29	0.45	0.14	0.15
EV-JRC	0.20	0.22	0.44	0.40	0.16	0.17
EV-IVM	0.15	0.37	0.20	0.27	*0.28*	*0.20*
JRC-IVM	0.19	*0.53*	*0.49*	*0.64*	0.26	0.11
Average	0.21	0.34	0.32	0.38	0.23	0.16

Table 6 - Map comparison statistics of individual ecosystem services and bundles. For each service, the highest (least similar) and lowest (most similar) map comparison statistic are indicated.

The *erosion protection* maps show no agreement in regions identified as a hotspot (Figure 20). A few regions show agreement between the coldspots for erosion protection, especially within strongly urbanised regions. This disagreement between the maps for this service is also reflected in the high minimum coefficient of variation (0.31, Table 7). On average, high erosion protection is expected in Scandinavia and the Alps, due to the high amount of natural vegetation. Low values are found in Hungary, the UK and parts of Spain. In most of the areas with a high average level of erosion protection, the variation among the estimates is large.

The *flood regulation* maps agree on hotspots in Scandinavia and coldspots in Hungary. High mean values are also found in large parts of Central Europe while low values dominate in the UK. In considerably large areas with low flood regulation, the maps are clearly in agreement.

The *recreation* service maps only show small areas of disagreement scattered across Europe. High values are seen along the coasts of the Mediterranean, in Scotland, Northern Spain and in Scandinavia. There is reasonable agreement on the values between the maps (Figure 21) with low coefficients of variation (Table 7).

High overall ecosystem service provision is expected in Scandinavia and parts of Southern Europe while a low provision of the selected services is seen in large urban areas, and in Hungary and England (Figure 21). The maps do agree on the areas with low values for the ecosystem service bundle. Agreement on areas with high provision of the total bundle is lower (Figure 20).

As shown in Figure 20, the erosion protection maps disagree in half of the area considered while (partial) agreement for recreation is highest.

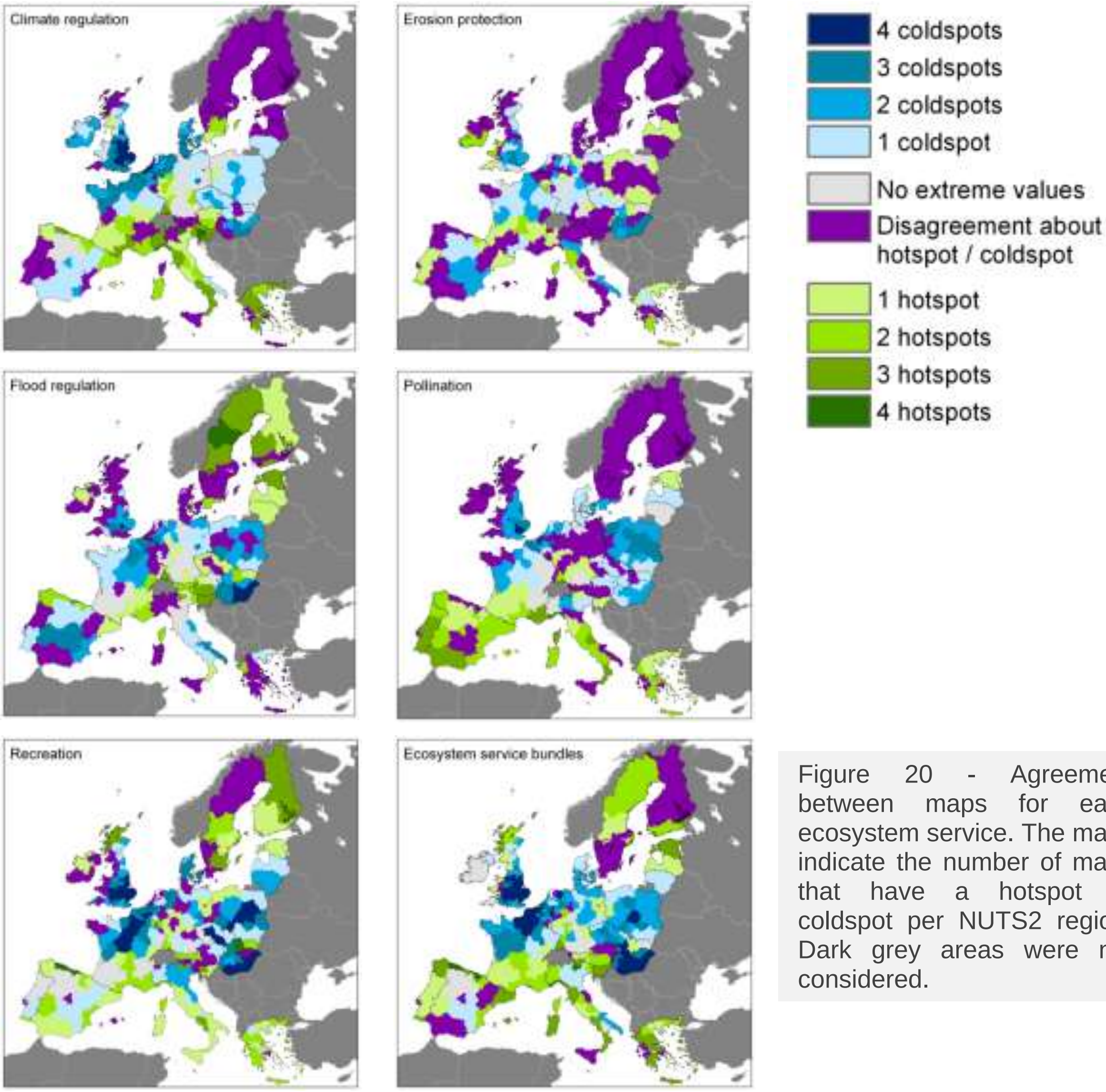

Figure 20 - Agreement between maps for each ecosystem service. The maps indicate the number of maps that have a hotspot or coldspot per NUTS2 region. Dark grey areas were not considered.

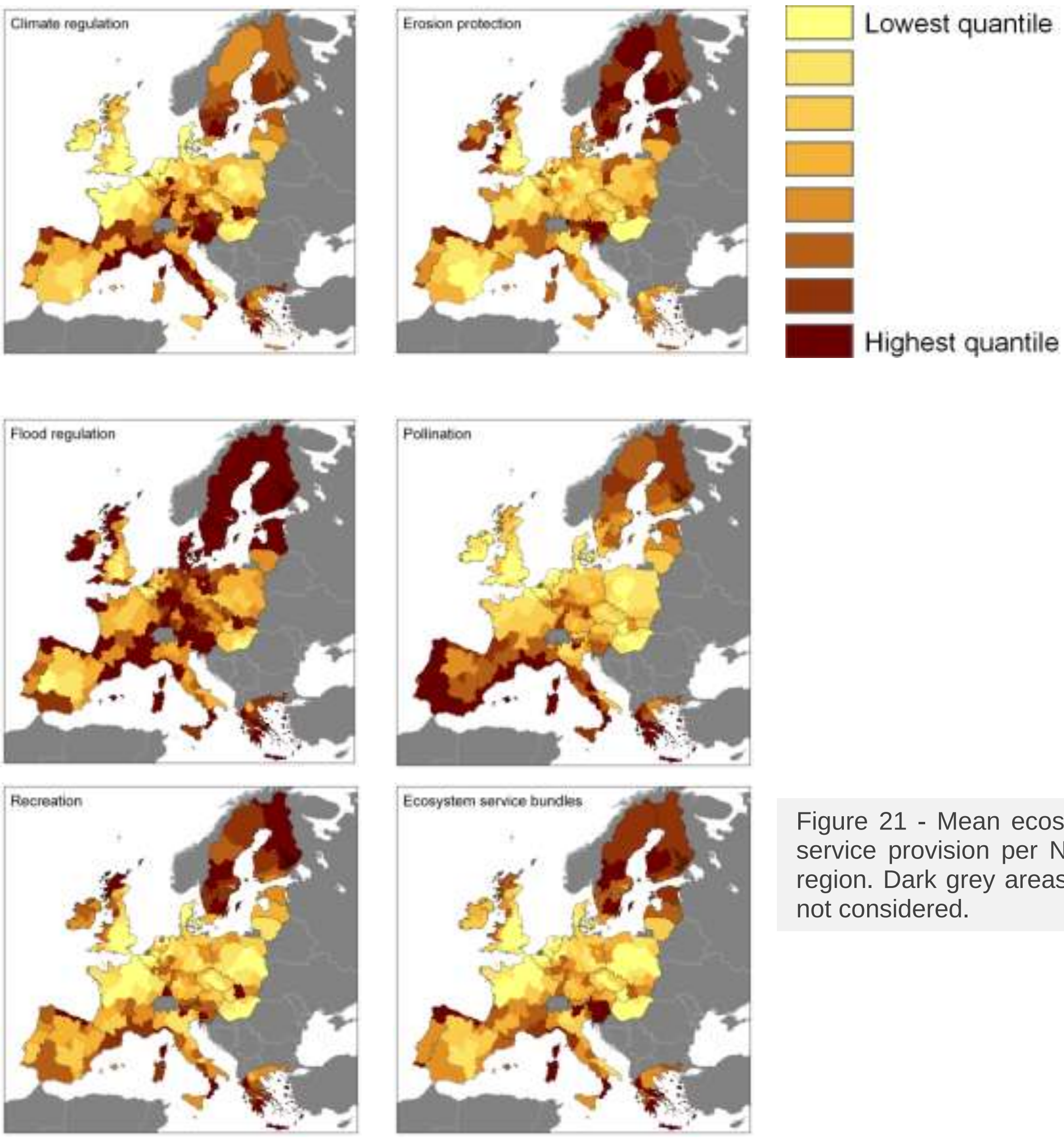

Figure 21 - Mean ecosystem service provision per NUTS2 region. Dark grey areas were not considered.

Table 8 summarizes correlations between the mean ecosystem service provision values and CVs, and the percentage per region covered by particular land cover types. The provision of all five ecosystem services is negatively correlated with areas covered by urban and arable land, and positively correlated with forests and natural areas. For all individual services, except recreation, the CVs are positively correlated with the area covered by built-up land, indicating that the maps disagree on the lower ecosystem service provision in urban areas. The maps agree on the high level of ecosystem service provision in forest areas, indicated by the negative correlations between CVs and forest areas. The positive correlations between CVs and arable land area indicate that the maps disagree on the ecosystem service provision in arable land, while for pasture the CV differs per service. In areas with more pasture, the maps disagree more on the provision of pollination and recreational services, while for the other services no relations were found.

Service	CV			
	Minimum	Location of low values	Maximum	Location of high values
Carbon	0.164	Germany	1.786	England, Scandinavia
Pollination	0.136	Greece, Spain, Portugal	1.516	Northwest Atlantic region
Erosion protection	0.306	Alpine and Pyrenees	1.318	Netherlands, Germany, UK
Flood regulation	0.090	Scotland, Ireland, Scandinavia, Portugal	1.373	Spain, Poland, Hungary
Recreation	0.039	Mediterranean, Germany, Estonia	1.000	Poland, Hungary, UK

Table 7 - Minimum and maximum coefficients of variation for NUTS2 regions between service estimates; low values indicate agreement between the different ES estimates, high values indicate large variation between reported values.

		Urban	*Pasture*	*Nature*	*Forest*	*Arable*
Carbon	Mean	-0.499	-0.120	0.311	0.777	-0.398
	CV	0.370	0.059	-0.123	-0.439	0.144
Pollination	Mean	-0.525	-0.077	0.438	0.455	-0.307
	CV	0.329	0.340	-0.379	-0.336	0.152
Erosion prevention	Mean	-0.570	0.254	0.304	0.583	-0.428
	CV	0.347	-0.093	-0.466	-0.424	0.548
Flood protection	Mean	-0.533	0.055	0.283	0.609	-0.321
	CV	0.256	-0.084	-0.248	-0.314	0.334
Recreation	Mean	-0.476	0.137	0.481	0.572	-0.570
	CV	-0.013	0.192	-0.292	-0.229	0.363
Bundle	Mean	-0.504	0.082	0.402	0.550	-0.420
	CV	-0.028	0.271	-0.078	0.234	-0.177

*: Urban: all artificial surfaces (CORINE classes 111-142). Pasture: CORINE class 231. Nature: scrublands, herbaceous vegetation and open spaces (CORINE classes 321-335). Forest: All coniferous / deciduous / mixed forests (CORINE classes 311-313). Arable: All rainfed and irrigated arable land (CORINE classes 211-213).

Table 8 - Correlations between area percentages of land cover classes* per NUTS2 region and mean and CV of ecosystem service provision.

3.2.5. Discussion

The considerable disagreement among spatial patterns of ecosystem service provision across Europe is an indication of the uncertainties in large-scale ecosystem service assessments. Several sources can contribute to these uncertainties. We describe the sources of uncertainty (classified after (Hou *et al.*, 2013)) :

1. Definition of the ecosystem service indicators: Different categorisations of ecosystem services are available; the Millennium Ecosystem Assessment (MA, 2005), the TEEB classification (De Groot *et al.*, 2010) and the CICES classification (Maes *et al.*, 2013a) being the most common. Differences in the definition of services in these classification systems cause that the same service does not necessarily address the same aspects (Hernández-Morcillo *et al.*, 2013, Villamagna *et al.*, 2013).
2. Level of process understanding: ecosystem services are supplied by ecosystems to humans through a variety of biophysical and socio-economic processes. Not all these processes are completely understood or quantified (Nedkov & Burkhard, 2012). Different levels of understanding and the inherent uncertainty in understanding leads to different quantification methods and different choices regarding the inclusion of determinants.
3. Aim of mapping: The objective for creating a map influences the selection of the most relevant indicators, the data that are used, and the parameterization of the models.
4. Data sources: An important data source for all ecosystem service maps are land cover data, but also several other biophysical or socio-economic data sources are used. Different data sources are often used for the same variable. Differences in input data propagate into differences in the resulting ecosystem service map.
5. Methodology: methodologies for mapping have different levels of complexity, ranging from process-based simulation to expert based value-transfer methods. Different methods result in different ecosystem service maps.

3.2.6. Conclusions

The protection and restoration of ecosystem services is an increasingly important policy. This study showed that a different definition of an ecosystem service or a different mapping approach could lead to contrasting spatial patterns of ecosystem service provision. The systematic comparison of four EU-scale maps of different ecosystem services demonstrated that there is an overall agreement among the climate regulation maps and the recreation potential maps. The erosion protection and flood regulation maps differed strongly, the pollination maps showed intermediate variation among the maps. Differences between the maps are caused by differences in the mapping aim, indicator definitions, input data and mapping approaches. The sources of uncertainty differ in their importance for the mapping of different ecosystem services. For services with larger differences in definition and mapping approaches, larger differences between individual maps emerge. Due to the lack of independent data on ecosystem service provision, ecosystem service maps cannot be properly validated and there are, so far, no appropriate measures for map quality.

The choice of a specific ecosystem service map to support policy will influence the specification of policy targets. Together with the lack of insight in ecosystem service map quality, varying map compilation as well as interpretation skills, this indicates that mapmakers as well end-users such as policy makers should be cautious when applying ecosystem service maps for decision making. Mapmakers need to clearly underpin the indicators used, the methods, and related uncertainties. Finally, there is an urgent need for better process understanding and data acquisition for ecosystem service mapping, modelling and validation.

4. Spatial modelling of marine ES: a new frontier

The ecosystem services (ES) framework is a valuable way to identify the benefits derived from nature and to link them to human well-being, additionally it provides an adequate setting for balancing human development with the preservation of the environment. In the marine environment, however, the application of the ES framework is hampered by the lack of extensive and detailed information on the distribution of habitats and the ecosystem functions they provide. Data and methods to assess the provision of services stemmed from the marine environment are far behind to those available for terrestrial environments (Barbier, 2012, Costanza, 1999). The gap is greatest when it comes to the mapping of ES, the main reasons behind this difference is the lack of resolution spatial information of habitat and species distribution and the incomplete understanding of ecosystem processes and functions within a highly dynamic three-dimensional environment with fluid boundaries (Maes *et al.*, 2012).

A recent review carried out by (Liquete *et al.*, 2013a) clearly summarizes current existing research on marine and coastal ecosystem services (MCES). The review uncovered a total of 145 studies related to MCES. This figure highlights how the assessment of marine and coastal ES is still at a very early infancy stage. Before year 2000, only 10 articles were published on MCES, from 1997 to 2006 the average rate of publication was 2.5 papers per year. After 2006, the annual publication rate rose to 23, possibly encouraged by the publication of the Millennium Ecosystem Assessment in 2005 (MEA, 2005). Over half of the reviewed papers were of quantitative nature and provided some type of quantitative indicators or measures. One tenth of the papers were qualitative assessments and were generally based on expert opinions or stakeholders preferences. And only four out of 154 papers were identified as mapping approaches (see (Costanza, 2008, Edwards *et al.*, 2010, Feagin *et al.*, 2010, Ruiz-Frau *et al.*, 2011). In terms of modeling, assessment tools such as InVEST (Integrated Valuation of Ecosystem Services and Trade-offs) offer new means to assess, map, model and value multiple services provided by marine ecosystems (Chan & Ruckelshaus, 2010, Tallis *et al.*, 2012). Marine InVEST maps and models ecosystem service flows and their changes under alternative management scenarios to elucidate the true costs and benefits of natural resource management options. The tool is applicable across multiple scales in coastal and marine regions with diverse habitats, policy questions, and stakeholders (Guerry et al 2012).

The search carried out as part of the present Deliverable for existing studies on mapping and modelling of MCES points in the same direction as Liquete's review, i.e. that the mapping and modelling techniques are still at a very early stage. Our search revealed a total of 22 studies; almost half of them (45%) focused on Regulation & Maintenance services, of those 45% concentrated on coastal protection (wind & flood protection) and 36% on carbon sequestration and storage. A third of the studies (32%) focused on provisioning services, particularly on food production (i.e. fish). The rest of the studies concentrated on cultural services. The classification of the studies according to the categories highlighted as part of this document revealed that 45% of the models were of a geo-statistical nature, 14% were phenomenological, 14% trait-based, 9% macro-ecological and only 4.5% process-based.

Recently, a technical report written by the European Commission provided what could be a key stepping stone for the advancement of the assessment and mapping of MCES (Maes *et al.*, 2014). The report presents a set of marine and coastal indicators to map and assess biodiversity, ecosystem condition and ecosystem services according to the Common International Classification of Ecosystem Services (CICES v4.3). This is fundamental as is only through the existence of an agreed set of indicators that the assessment and mapping of ES will be able to progress. Appendix 1 - Table 2a - Part 1 presents the indicators to assess MCES.

Additionally, in order further existing research on MCES it is necessary to address several fundamental questions:

- Role of biodiversity as a base for ecosystem processes: there needs to be a clear understanding of the relationships between biodiversity and ecosystem functions in marine ecosystems.
- There is a lack of information at which scales ecosystem processes and functions occur and how these relate to the provisioning of services.
- There is an urgent need for high quality geo-referenced data (i.e. habitat mapping).

5. Conclusion and future plans

In order to achieve the ambitious agenda set by the EU Biodiversity Strategy Action 5, and to support sustainable development that both preserves and benefits from natural capital and ecosystem services, considerable progress is still needed in the practice of quantifying ecosystem service supply. Today a rich array of methods are available, especially for terrestrial systems, that enable the incorporation of biodiversity effects on ecosystem functioning into quantitative, spatially-explicit assessments of ecosystem service supply. In Deliverable 3.1 we have summarised the main characteristics, strengths and weaknesses of different approaches, highlighting their complementarity depending on scale, assessment objectives and context, available skills and data. The planned used of different types of models for a selection of OPERAs Examplars illustrates the predominant effect of scale on model selection, and the ability within a single case study to combine different model types, of varying complexity and detail in the representation of biodiversity effects, depending on specific ES of interest, skills and data / resources availability. Besides, model categories are not necessarily exclusive and there may be more of a continuum between approaches. Recent model developments, with innovative hybridization across model types illustrate how increasing fundamental understanding on the role of different facets of biodiversity for ecosystem functioning and ecosystem services can be incorporated into the spatially explicit modelling of ecosystem service supply. As the availability of biodiversity data (species, phylogenetic and functional) increases and the potential for remote sensing of taxonomic and functional diversity becomes realised, the application of more ‘biodiversity realistic’ models should be able to move to from research to practice. Considerable challenges remain for the practice of assessments to embrace good practice in model uncertainty quantification and validation, an upstream research need to still be addressed. Lastly, while the mapping of terrestrial ecosystem service supply is now reaching greater maturity, for marine ecosystems research is still in its infancy. Urgent research needs regard a better understanding of marine biodiversity effects on ecosystem functioning, and at which scales this influences ecosystem service supply. The availability of high resolution data also proves to be an obstacle that needs to be cleared before sound practice can be achieved.

This Deliverable is intended to be a living document, to be updated as WP3.1 research progresses in the development and implementation of improved geo-referenced metrics and GIS based quantification functions of terrestrial and marine ecosystem service supply. The endpoint will be the submission of a journal paper (Milestone 13.3) at month 36.

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Appendix 1

Appendix 1 - Table 1a - Part 1 - Terrestrial Model Variables

Model name	Partner	Ecosystem service	Model type	Scale(s) of applicability	Land cover
		(CICES terminology)		local / regional / continental…	classification and data source
IVM-carbon (Schulp et al, 2008)	VU-IVM	Global climate regulation	Phenomenological	continental (EU)	CLUE
IVM-pollination (Schulp et al, 2014)	VU-IVM	Pollination	Phenomenological	applied at continental (EU) (NUTS2-regions). Model run on 250x250 LC data CORINE	CORINE and additional linear element dataset (van der zanden et al., 2013)
IVM-tourism (Van Berkel & Verburg, 2011)	VU-IVM	Physical use of land-/seascapes	Phenomenological	continental (EU)	CORINE land cover
Biocontrol (Civantos et al. 2012)	CNRS-LECA	Biocontrol	Macroecological	regional - continental (EU)	CORINE land cover 2000 - although any data base is suitable in principle
Trait-based models of grassland ES (Lavorel et al. 2011, Grigulis et al. 2013)	CNRS-LECA	Grassland forage quantity, forage quality, soil organic matter, leached nitrates, soil fertility, soil stability	Trait-based	landscape	grassland management types

LPJ-GUESS **(Smith et al. 2001, Sitch et al. 2003).** **Further developments e.g. in Lindeskop et al. (2013), Smith et al. (2013)**	KIT	Global climate regulation, surface water supply (non-drinking), cultivated crops, fodder; tested: timber, energy crops, soil formation, etc.	Process-based	regional/global	Historical and fand-use fractions according to Hurtt et al. 2011, crop species according to MIRCA2000 (Portman et al., 2010) . Usage of CLUMondo tested (translation envisaged in Global Exemplar)
LPJmL **(Bondeau et al. 2007)** **Further developments in: Rost at al. 2008,** **Rost et. 2009,** **Müller et al. 2009, Gumpenberger et al. 2010, Fader et al. 2010,** **Beringer et al. 2011, Biemans et al. 2011,** **Popp et al. 2011,** **Popp et al. 2012,** **Waha et al. 2012, Schaphoff et al. 2013, Waha et al. 2013.**	IMBE	Provisioning (cultivated crops, fodder grass, fibres, timber, energy plants, non-drinking surface water), Regulation and maintenance (vegetation cover protecting, hydrological cycle and water flow maintenance, soil formation, global and regional climate regulation)	Process-based	regional / global	1) specifically adapted LPJmL historical land use data set (Fader et al. 2010), derived from the combination of MIRCA 2000 (Portmann et al. 2010), cropland and pasture fractions (Ramankutty et al. 2008), and historical land cover (Klein Goldewijk & van Drecht 2006). Spatial resolution: 0.5° global, 0.25° regional, finer if needed. 2) for the future: published land use projections or simulated land use from the bio-economic MAgPIE model feeded by LPJmL (Lotze-Campen et al. 2008, 2010)
IVM-FloodRegulation **(Stürck et al, 2014)**	VU-IVM	Flood protection	Process-based	continental (EU)	CORINE land cover 2000

SWAT	UBO, UFZ	Cultivated crops, fibres and other materials from crops for direct use or processing (biofuel), Hydrological cycle and water flow maintenance, Mass stabilisation and control of erosion rates, Chemical condition of freshwaters, surface water for drinking, ground water for drinking,surface water for non-drinking purposes, ground water for non-drinking purposes	Process-based	regional	Any classification is suitable, it needs to be linked to the entries in the crop type database which contains generic land use classes and individual crops
HILLFLOW (Leitinger et al. in review)	CNRS-LECA (coll. UIBK)	Soil moisture, deep water seepage	Process-based	landscape	grassland management types

Appendix 1 - Table 1a - Part 2 - Terrestrial Model Variables

Model name	**Partner**	**Abiotic variables**			
		climate	***soil***	***landscape pattern***	***others***
IVM-carbon (Schulp et al, 2008)	VU-IVM		emission factors: Map with emission factor for each land use type as 1x1 km grids (see calculation rules) (Janssens et al., 2005) & Forest emission factors for soil and biomass from EFISCEN simulations		Map of forest biomass carbon content per EFISCEN region
IVM-pollination (Schulp et al, 2014)	VU-IVM				
IVM-tourism (Van Berkel & Verburg, 2011)	VU-IVM			Classification of the landscape relief within a 10km radius	tourist infrastructure; accesibility; policy instruments; tourist attractions; local cooperative networks; NGO operation and cooperation
Biocontrol (Civantos et al. 2012)	CNRS-LECA	monthly precipitation, temperature (min, max, mean), ETP, aridity index. Data from alternative data bases or climate scenarios (variable spatial resolution)			

Trait-based models of grassland ES (Lavorel et al. 2011, Grigulis et al. 2013)	CNRS-LECA		soil texture (calculation of water holding capacity), soil depth, soil C, soil N	DEM: altitude
LPJ-GUESS (Smith et al. 2001, Sitch et al. 2003). **Further developments e.g. in Lindeskop et al. (2013), Smith et al. (2013)**	KIT	Daily or monthly average air surface temperature, precipitation (daily precipitation or monthly precipitation and wet days), incoming shortwave radiation (or sunshine hours per day). Various sources depending on scale and considered time frame, e.g. 0.5° from CRU TS 3.1 (Mitchell and Jones 2005), usually in combination with CMIP5 scenario climate data (e.g. MPI-ES-LR after Giorgetta et al., 2013).	global soil map (FAO, 1991)	atmospheric CO2 concentration
LPJmL (Bondeau et al. 2007) Further developments in: Rost at al. 2008, Rost et. 2009, Müller et al. 2009, Gumpenberger et al. 2010, Fader et al. 2010, Beringer et al. 2011, Biemans et al. 2011, Popp et al. 2011, Popp et al. 2012, Waha et al. 2012, Schaphoff et al. 2013, Waha et al. 2013.	IMBE	Daily or monthly average air surface temperature, daily precipitation (or monthly precipitation and wet days), cloudiness or shortwave and longwave radiation. Various sources depending on the scale, e.g. 0.5° from CRU TS 3.1 (Mitchell and Jones 2005) and GPCC (Rudolf et al 2010), 0.25° from WATCH Forcing Data (Weedon et al. 2011) and ERA-Interim (ECMWF).	Harmonized World Soil Database (version 1.2) (2012) aggregated to 0.5◦ resolution and classified according to the USDA soil texture classification (http://edis.ifas.ufl.edu/ ss169).	atmospheric CO2 concentration

IVM-FloodRegulation (Stürck et al, 2014)	VU-IVM	precipitation regime (Haylock et al., 2008)	soil water holding capacity classification (FAO, 2009)		DEM and forest and agricltural management variables
SWAT	UBO, UFZ	precipitation, temperature (min and max), solar radiation, wind speed, humidity, potential evapotranspiration, daily resolution, spatial resolution: climate stations. Depending on the method used to calculate evapotransipiration. Values can also be estimated using a weather generator.	number and thickness of layers, hydrologic soil class, soil porosity, saturated hydraulic conductivity, porosity, field capacity, water content at wilting point, clay/silt/sand content, organic matter content, bulk density,… available resolution of soil together with land cover resolution defines the achiveable resolution		terrain (slope)
HILLFLOW (Leitinger et al. in review)	CNRS-LECA (coll. UIBK)	precipitation, temperature (min and max), solar radiation, wind speed, humidity, potential evapotranspiration, daily resolution, spatial resolution: climate stations.	soil texture, saturated water content, field capacity, residual soil water content, saturated hydraulic conductivity, soil depth, macropores		DEM: altitude, slope, aspect

Appendix 1 - Table 1a - Part 3 - Terrestrial Model Variables

Model name	**Partner**	**Biotic variables**					
		individual species	***species diversity indices***	***Plant Functional Types***	***Plant Funct. Traits***	***functional diversity indices***	***others***
IVM-carbon (Schulp et al, 2008)	VU-IVM						forest age
IVM-pollination (Schulp et al, 2014)	VU-IVM						pollination dependency index per crop; Habitat suitability for bees
IVM-tourism (Van Berkel & Verburg, 2011)	VU-IVM						biophysical characteristics (e.g., presence of sea, beach); presence of N2000 areas, HNV famrland, and UNESCO natural monuments
Biocontrol (Civantos et al. 2012)	CNRS-LECA	vertebrate species known as predators of vertebrate or invertebrate pests					
Trait-based models of grassland ES (Lavorel et al. 2011, Grigulis et al. 2013)	CNRS-LECA		plant Shannon diversity			plant community mean vegetative height, leaf N concentration, leaf dry matter content, rooting	microbial functional diversity parameters calculated from plant traits and soil N and WHC

			architecture
LPJ-GUESS **(Smith et al. 2001, Sitch et al. 2003).** **Further developments e.g. in Lindeskop et al. (2013), Smith et al. (2013)**	KIT	11 PFTs e.g. according to Ahlstöm et al. (2012); 11 CFTs (Lindeskog et al. 2013)	
LPJmL (Bondeau et al. 2007) **Further developments in: Rost at al. 2008,** **Rost et. 2009,** **Müller et al. 2009,** **Gumpenberger et al. 2010, Fader et al. 2010,** **Beringer et al. 2011, Biemans et al. 2011,** **Popp et al. 2011,** **Popp et al. 2012,** **Waha et al. 2012, Schaphoff et al. 2013, Waha et al. 2013.**	IMBE	9 PFTs (Sitch et al. 2003), 12 annual CFTs, 2 types of managed grass, 3 types of bioenergy plants. In progress: perenial crops.	

IVM-FloodRegulation (Stürck et al, 2014)	VU-IVM						tree species, as part of the forest management variables at 1km scale (Brus et al. 2012)
SWAT	UBO, UFZ						The crop.dat we use contains currently 17 generic land use types with vegetation cover (such as pasture, rangeland, decidious forest), 81 agricultural crops. But this list has been extended e.g. for applications in the tropics.
HILLFLOW (Leitinger et al. in review)	CNRS-LECA (coll. UIBK)					community mean root depth, evapo-transpiration, canopy interception	

Appendix 1 - Table 1b - Part 1 - Terrestrial Model Applications

Model name	Partner	Ecosystem service (CICES terminology)	Model type	Brief description of model logics
IVM-carbon (Schulp et al, 2008)	VU-IVM	Global climate regulation	Phenomenological	The carbon sequestration effect of land use change scenarios is tested at the EU scale. Each land cover category is assigned an annual average effect on carbon sequestration per country. For forest carbon seuqestration is weighted by calculation of forest age, for agriculture a SOC map is used to weigh the effects of agriculture on carbon sequestration
IVM-pollination (Schulp et al, 2014)	VU-IVM	Pollination	Phenomenological	potential supply of pollination is mapped based on habitat suitability of different land covers. Visitation probability is then calculated based on distance from landscape elements providing habitat using a distance decay function. Demand for pollination is mapped based on pollination dependency of crops. In the last step actual supply is then determined based on an overlay of pollination potential supply and pollination demand.
IVM-tourism (Van Berkel & Verburg, 2011)	VU-IVM	Physical use of land-/seascapes	Phenomenological	expert based assessment of rural development options in Europe including rural tourism. Rural tourism is assessed based on suitability for summer tourism, winter tourism and nature tourism. These three factors areweighted by a factor for symbolic capital.
Biocontrol (Civantos et al. 2012)	CNRS-LECA	Biocontrol	Macroecological	macro-ecological model of the distribution of vertebrates that exert predation on vertebrate or invertebrate pests
Trait-based models of grassland ES (Lavorel et al. 2011, Grigulis et al. 2013)	CNRS-LECA	grassland forage quantity, forage quality, soil organic matter, leached nitrates, soil fertility, soil stability	Trait-based	statistical models of ecosystem properties depending on soil parameters, plant traits and their variations in response to soil and altitude

LPJ-GUESS (Smith et al. 2001, Sitch et al. 2003)	KIT	Global / regional climate regulation, surface water supply (non-drinking), cultivated crops; tested: timber, energy crops, soil formation, etc.	Process-based	LPJ-GUESS DGVM simulates development of land vegetation and biogeochemical cycles. Output variables are used to derive current state of selected Ecosystem Services and their historical and future transitions, e.g. carbon, nitrogen and water cycles, potential crop yields, that are translated into various Ecosystem Services
LPJmL (Bondeau et al. 2007)	IMBE	Provisioning (cultivated crops, fodder grass, fibres, timber, energy plants, non-drinking surface water), Regulation and maintenance (vegetation cover protecting, hydrological cycle and water flow maintenance, soil formation, global and regional climate regulation)	Process-based	Process-based agro-ecosystem model: simulates the distribution of the potential natural vegetation, carbon stocks, carbon and water cycles, crop yields, harvested biomass. Climate- and management-driven outputs translate into a range of Ecosytem Services.
IVM-FloodRegulation (Stürck et al, 2014)	VU-IVM	Flood protection	Process-based	The STREAM hydrologial model is applied to several catchements across the EU. Precipitation data is linked to soil and land cover classes across the catchments resulting in a flood regulation supply index. The flood regulation supply is compared between current and potential vegetation (based on Foley & Ramankutty, 1999) to determine target areas where vegetation could enhance flood regulation supply

SWAT	UBO, UFZ	Cultivated crops, fibres and other materials from crops for direct use or processing (biofuel), Hydrological cycle and water flow maintenance, Mass stabilisation and control of erosion rates, Chemical condition of freshwaters, surface water for drinking, ground water for drinking,surface water for non-drinking purposes, ground water for non-drinking purposes	Process-based	SWAT is a physically-based, conceptual, continuous-time river basin model with spatially semi-distributed parameters operating on a daily time step. It was designed to simulate broader scale patterns of discharge and water quality in the spatial and temporal domain (Neitsch et al., 2005b). The model integrates all relevant processes for watershed modeling including water flow, nutrient transport and turnover, vegetation growth, land use, and water management at the sub-basin scale. It considers five different pools of nitrogen in the soils (Neitsch et al., 2005b): two inorganic (ammonium and nitrate) and three organic (fresh organic nitrogen and active and stable organic nitrogen). Nitrogen is added to the soil by fertilizer, manure or residue application, fixation by bacteria, and atmospheric deposition. Nitrogen losses occur by plant uptake, leaching, volatilization, denitrification and erosion.
HILLFLOW (Leitinger et al. in review)	CNRS-LECA (coll. UIBK)	Soil moisture, deep water seepage	Process-based	Mechanistic model of water evaporation, lateral flow and deep seepage depending on vegetation demand, soil properties and terrain

Appendix 1 - Table 1b - Part 2 - Terrestrial Model Applications

Model name	Partner	Main strengths	Limitations	Existing applications (other than OPERAs)	Use in Examplars (cite examplar)	Literature reference(s)
IVM-carbon (Schulp et al, 2008)	VU-IVM	able to detect changes in carbon sequestration following land use change at coarse levels; applicalbe across many EU countries;	use of country level averages per land cover class; focused on mapping changes and not necessarily state; only applicable at country or coarser level; only applicable in the EU four countries incorporated in study Janssens et al. (2005)		European, Scotland	Schulp et al. 2008 Agriculture, Ecosystems & Env 127:251–264
IVM-pollination (Schulp et al, 2014)	VU-IVM	incorporation of both mapping demand and supply; applicable across many regions; level of detail can be nehanced by parameterizing the model for individual species	difficult to validate results, assumption of habitat uniformity, variation in timing of pollination demand and supply within a year not accounted for		European, Scotland	Schulp et al. 2014 Ecological Indicators 36:131-141

IVM-tourism (Van Berkel & Verburg, 2011)	VU-IVM	Applicable across the EU; using easy accesible datasets	Only applicable at this scale; expert based approach makes it inherently subjective; preferences and suitable indicators might change over time; dos not generate reliable results in all regions		European, Scotland	Van Berkel & Verburg, 2011 Land Use Policy 28:447-459
Biocontrol (Civantos et al. 2012)	CNRS-LECA	Climate- and land use-based distributions of service providing species. Easy to project given scenarios. Contribution of individual species may be combined with different weights e.g. depending on diets (although currently even weights)	Usual limits of species distribution modelling	Estimation of projected biocontrol under future climate (Civantos et al. 2012) or land use (VOLANTE) scenarios	TBA	Civantos, E., Thuiller, W., Maiorano, L., Guisan, A. & Araújo, M.B. (2012) Potential Impacts of Climate Change on Ecosystem Services in Europe: The Case of Pest Control by Vertebrates. BioScience, 62, 658-666.

Trait-based models of grassland ES (Lavorel et al. 2011, Grigulis et al. 2013)	CNRS-LECA	Mechanistic understanding of ES supply; functional understanding of ES trade-offs / bundles. Easy to project given scenarios.	Generic nature of models under checking (inter-site comparison). May need adaptation for different bioclimatic regions	Scenario projections under drought and socio-economic change for the French Alps	French Alps (grasslands only)	Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.-P., Garden, D., Girel, J., Douzet, R. & Pellet, G. (2011) Using plant functional traits to understand the landscape-scale distribution of multiple ecosystem services. Journal of Ecology, 99, 135-147. Grigulis, K., Lavorel, S., Krainer, U., Legay, N., Baxendale, C., Dumont, M., Kastl, E., Arnoldi, C., Bardgett, R., Poly, F., Pommier, T., Schloter, M., Tappeiner, U., Bahn, M. & Clément, J.-C. (2013) Combined influence of plant and microbial functional traits on ecosystem processes in mountain grasslands Journal of Ecology, 101, 47-57. Lamarque, P., Lavorel, S., Mouchet, M. & Quétier, F. (2014) Plant trait-based models identify direct and indirect effects of climate change on bundles of grassland ecosystem services. Proceedings of the National Academy of Sciences, in press.

LPJ-GUESS (Smith et al. 2001, Sitch et al. 2003)	KIT	Global quantification; historical and future transitions; high detail in representation of vegetation dynamics (age cohorts and gap dynamics), closed carbon and nitrogen cycles	Limitations in resolution (0.5°x0.5°), applicable up to contry/regional level (i.e. Downscaling aspired in Scottish Exemplar)	Simulation of ecosystem state and processes, e.g. carbon balances, BVOC fluxes, etc.	Global, Scotland, maybe European	Smith et al. 2001, Glob. Ecol. And Biogeography; Sitch et al. 2003, Glob. Change Biology
LPJmL (Bondeau et al. 2007)	IMBE	Closed carbon cycle, consistent representation of the biogeochemical processes bewteen the different plant types.	Currently no nitrogen cycle	Land use modelling, agricultural water footprints, land use-climate feedbacks, HANPP trajectories, food security, etc	Mediterranean (ev. European) region: Different trade-offs future trajectories are provided from simulations accounting for climate projections and management scenarios, delivering relevant informations for stake-holders.	

IVM-FloodRegulation (Stürck et al, 2014)	VU-IVM	Combination of flood regulation demand and supply to identify prioritiy areas where flood regulation can be enhanced using natural vegetation.	Extrapolation of estimates for relation between land cover, soils and flood regulation from single catchments to the entire EU. Method is difficult to apply at smaller scales		European, Scotland	Sturck et al. 2014 Ecological Indicators 38: 198-211
SWAT	UBO, UFZ	Detailed representation of crop management; high number of management options implemented	Limited for the modelling of forests - focus is on the modelling of agricultural systems. Suitable for the regional scale (watersheds > ~ 50 sqkm), not suitable for small watersheds.	Estimation of trade-offs between increasing bioenergy production, food & fodder production,water provisioning and water quality. Effects of management options on water quality. Effects of land use and climate change secarios on water quality regulation and water provisioning	-	Lautenbach, S., J. Maes, M. Kattwinkel, R. Seppelt, M. Strauch, M. Scholz, C. Schulz-Zunkel, M. Volk, J. Weinert, and C. F. Dormann. 2012. Mapping water quality-related ecosystem services: concepts and applications for nitrogen retention and pesticide risk reduction. International Journal of Biodiversity Science, Ecosystem Services & Management 8:35–49.

HILLFLOW (Leitinger et al. in review)	CNRS-LECA (coll. UIBK)	Mechanistic understanding of ES supply depending on vegetation functioning	Not a detailed hydrological model; requires heavy site measurements for parameterisation	Scenario projections under drought and socio-economic change for the French Alps and the Stubai Valley (Austria)	French Alps (grasslands only)	Leitinger, G., Ruggenthaler, R., Hammerle, A., Lavorel, S., Lamarque, P., Schirpke, U., Clément, J.C., Obojes, N. & Tappeiner, U. (submitted) Drought impact on water provision of managed alpine grasslands in two climatically different regions of the Alps. Ecohydrology.

Appendix 1 - Table 2a - Part 1 - Marine Model Variables

Model name	**Partner**	**Ecosystem service**	**Model type**	**scale(s) of applicability**	**Land cover**
		(CICES terminology)		local / regional / continental…	classification and data source
Ecosim/EcoPath (Alcamo et al, 2005)	CSIC	Provisioning, nutrition, biomass (fish production)	Macroecological	regional	NA
Mercury sequestration (Anastacio et al 2013)	CSIC	Mediation of waste, toxics and other nuisances	Process-based	regional	NA
Barbier 2012	CSIC	mediation of flows (storm protection) & fish density	NA	local	NA
hydrodynamic model (Temmerman et al 2012)	CSIC	Mediation of flows (flood protection)	Phenomenological	local	NA
hydrodynamic model (Shepherd et al 2007)	CSIC	Maintenance of physical, chemical and biological conditions (nutrient removal and carbon sequestration)	Phenomenological	local	NA
bioeconomic model (Sanchirico and Springborn 2011)	CSIC	Provisioning, nutrition, biomass (fish production)	NA	local/regional	NA
mangrove's wind protection (Das et al, 2013)	CSIC	Mediation of flows (wind protection)	Phenomenological	regional	NA
CO2 capture potential of seagrass restoration (Duarte et al, 2013)	CSIC	Maintenance of physical, chemical and biological conditions (carbon sequestration)	Trait-based	local	NA

economic/ecological model (Eichner &Tschirhart, 2006)	CSIC	food production & non-consumptive use of popular species, naturalness	Macroecological	regional	NA
Multiscale ecological and economic models salmon, shrimp & blue crab (Jordan et al 2012)	CSIC	Provisioning, nutrition, biomass (food production)	Phenomenological	local & regional	NA
Recreation model (Kreitler et al 2013)	CSIC	Cultural (recreation)	NA	regional	NA
InVEST (Guerry et al 2012)	CSIC	multiple ES (renewable energies, food from fisheries and aquaculture, coastal protection, aesthetic, recreation and carbon storage and sequestration.	Spatial proxy-based	multiple scales	NA
Ecological-economic model (Leslie et al, 2009)	CSIC	Provisioning, nutrition, biomass (Fisheries)	Trait-based	local	NA
Coastal protection (Liquete et al 2013)	CSIC	coastal protection	Spatial proxy-based	continental (EU)	Three data sources: EU Corine Land Cover (CLC) dataset v.15 from the year 2000 with a resolution of 100 m (EEA 2011); and modelled seabed habitat maps (MESH 2010; EUSeaMap JNCC 2010)

Role of eelgrass in ES, food web modeling (Plummer et al 2013)	CSIC	multiple ES (provisioning, cultural, supporting)	Spatial proxy-based	local	NA
InVEST Marine carbon storage & sequestration (Guerry et al 2012)	CSIC	Carbon storage & sequestration	Spatial proxy-based	local / regional / continental	NA
InVEST Food provision (Guerry et al 2012)	CSIC	Food provision	Spatial proxy-based	local / regional / continental	NA
InVEST Marine renewable energy (Guerry et al 2012)	CSIC	Energy	Spatial proxy-based	local / regional / continental	NA
InVEST Recreation (Guerry et al 2012)	CSIC	Recreation	Spatial proxy-based	local / regional / continental	
Spatial PREdiction of benthic HABitats in the Baltic Sea (PREHAB) (Lindegarth et al 2014)	CSIC	Food provision	Spatial proxy-based	local/regional	NA
Spatially explicit economic assessment of cultural ecosystem services (Ruiz-Frau et al 2013)	CSIC	Recreation, Food provision	Spatial proxy-based	regional	NA

Mapping outdoor recreationists' perceived social values for ecosystem services at Hinchinbrook Island National Park, Australia (van Riper et al 2012)	CSIC	Recreation	Spatial proxy-based	regional	NA
Temporal variability in the benthos: Does the sea floor function differently over time? (Frid 2011)	CSIC	Food provision, carbon cycling and nutrient regeneration	Trait-based	local	NA

Appendix 1 - Table 2a - Part 2 - Marine Model Variables

Model name	**Partner**	**Abiotic variables**			
		climate	***soil***	***landscape pattern***	***others***
Ecosim/EcoPath (Alcamo et al, 2005)	CSIC	x			Economic development, greenhouse emissions, air pollution emission, risk of acidification and excess nitrogen emissions, climate change, sea level rise, nitrogen loading to coastal marine systems
Mercury sequestration (Anastacio et al 2013)	CSIC				Hg in biomass (several variables, Hg in belowground biomass, Hg exiting biomass, incorporation 365 days ago…), temperature, salinity, cloud cover
Barbier 2012	CSIC				Distance to the ecosystem, threat of ecological collapse
hydrodynamic model (Temmerman et al 2012)	CSIC	x		x	
hydrodynamic model (Shepherd et al 2007)	CSIC		x	x	Elevation; management variables;
bioeconomic model (Sanchirico and Springborn 2011)	CSIC			x	Habitat conversion (e.g. Mangroves to aquaculture ponds)
mangrove's wind protection (Das et al, 2013)	CSIC	x			% damaged houses, impact of the storm, wind velocity, velocity of the storm surge, suge height, distance from the coast
CO2 capture potential of seagrass restoration (Duarte et	CSIC	x			

al, 2013)					
economic/ecological model (Eichner &Tschirhart, 2006)	CSIC				Harvesting, consumption of a good, state of the ecosystem
Multiscale ecological and economic models salmon, shrimp & blue crab (Jordan et al 2012)	CSIC				Fishery landings, effort data, habitat GIS coverages, survival rates for habitat types, salinity, economic value salmon fisheries
Recreation model (Kreitler et al 2013)	CSIC				Visitation data, travel distance and demand, water quality, precipitation data, type of access to the park, park size, beach length, park actitivites and concessions, number of campsites, travel time
InVEST (Guerry et al 2012)	CSIC				Not specified
Ecological-economic model (Leslie et al, 2009)	CSIC				Fishing effort in sports and artisanal fishery, returns for both fisheries, price per unit of fish, price per tourist that fishes on a fishing boat, cost of fishing for artisanal and price for taking a tourist on a boat sportfshing, number of tourists involved in sportfishing
Coastal protection (Liquete et al 2013)	CSIC				Bathymetry, topography, slope, geomorphology, submarine habitats, emerged habitats, wave regime, tidal range, relative sea level, storm surge, population density, infrastructures, artificial surface, main cultural sites
Role of eelgrass in ES, food web modeling (Plummer et al 2013)	CSIC				

InVEST Marine carbon storage & sequestration (Guerry et al 2012)	CSIC				Carbon stored, rate of C accumulation in sediments, economic information such as market/non-market value of stored/sequestered Carbon
InVEST Food provision (Guerry et al 2012)	CSIC				Fishing fleet distribution, value of landings, fishing grounds distribution, price of harvestd product, harvest rate information
InVEST Marine renewable energy (Guerry et al 2012)	CSIC	wave condition data (height, peak period, technological capabilities (e.g. Performance tables, maximum capacity)			
InVEST Recreation (Guerry et al 2012)	CSIC	visitation rates, recreational activities			
Spatial PREdiction of benthic HABitats in the Baltic Sea (PREHAB) (Lindegarth et al 2014)	CSIC	water transparency			Shoreline exploitation, economic valuation assessed using the willingness to pay" method
Spatially explicit economic assessment of cultural ecosystem services (Ruiz-Frau et al 2013)	CSIC				Eonomic and social assessment

Mapping outdoor recreationists' perceived social values for ecosystem services at Hinchinbrook Island National Park, Australia (van Riper et al 2012)	CSIC				Slope, Distance to Trails, Distance to Water, Great Barrier Reef Marine Park waters, Queensland Parks and Wildlife Service waters, Social value points, roads, Hinchinbrook Towns, coastline
Temporal variability in the benthos: Does the sea floor function differently over time? (Frid 2011)	CSIC				

Appendix 1 - Table 2a - Part 3 - Marine Model Variables

Model name	Partner	Biotic variables						
		individual species	***species diversity indices***	***Plant Functional Types***	***Plant Functional Traits***	***Functio-nal diversity indices***	***others***	**Ecosystem type**
Ecosim/EcoPath (Alcamo et al, 2005)	CSIC	x					Thropic flows, biomass, production, mortality, exports, biomass accumulation, biomass of functional groups, consumption, catch data, thropic behaviours, landings, discards, fishing effort, human population development	marine
Mercury sequestration (Anastacio et al 2013)	CSIC							tidal wetlands
Barbier 2012	CSIC							
hydrodynamic model (Temmerman et al 2012)	CSIC			tidal wetlands				tidal wetlands
hydrodynamic model (Shepherd et al 2007)	CSIC							tidal wetlands and mudflats (estuary)

bioeconomic model (Sanchirico and Springborn 2011)	CSIC	fish species		mangrove forests; seagrass meadows; coral reefs			fishing; co-benefits of habitat conservation	mangrove forests; seagrass meadows; coral reefs
mangrove's wind protection (Das et al, 2013)	CSIC	x		mangrove forest			distance from mangrove forest, mangrove forest extent	mangrove forest
CO2 capture potential of seagrass restoration (Duarte et al, 2013)	CSIC	x		seagrass meadows			patch growth, parch survival in seagrass planting projects, estimates of seagrass CO2 sequestration per unit area for five seagrass species	seagrass meadows
economic/ecological model (Eichner &Tschirhart, 2006)	CSIC	x					biodiversity divergence, general equilibrium ecosystem model, population densities	marine
Multiscale ecological and economic models salmon, shrimp & blue crab (Jordan et al 2012)	CSIC	x					stock biomass, net recruitment per year, carrying capacity	marine
Recreation model (Kreitler et al 2013)	CSIC							marine

InVEST (Guerry et al 2012)	CSIC						not specified	marine
Ecological-economic model (Leslie et al, 2009)	CSIC	x					abundance of juvenile and adult snappers, time, larval fish recruit to juvenile populations, competitive effects among the young of the year, juvenile survival, total natural mortality, probability of bycatch mortality due to industrial shrimp fishery, probability of immigration to the adult population	marine
Coastal protection (Liquete et al 2013)	CSIC							marine
Role of eelgrass in ES, food web modeling (Plummer et al 2013)	CSIC						biomass, growth efficiency, consumption rates of prey, immigration rate, mortality, emigration rate, biological groups (primary producers, invertebrates, fishes, birds, marine mammals, detrital pools), commercial and recreational fisheries	marine
InVEST Marine carbon storage & sequestration (Guerry et al 2012)	CSIC						vegetation distribution maps	
InVEST Food provision (Guerry et al 2012)	CSIC						fish distribution, fish survival, recruitment rate	

InVEST Marine renewable energy (Guerry et al 2012)	CSIC							
InVEST Recreation (Guerry et al 2012)	CSIC						habitat distribution	
Spatial PREdiction of benthic HABitats in the Baltic Sea (PREHAB) (Lindegarth et al 2014)	CSIC	Fucus vesiculosus, eelgrass, Perca fluviatilis, Sander lucioperca		eelgrass, macroalgae			species (fish, macroalgae, eelgrass) distribution, fish recrutiment, stock size	marine
Spatially explicit economic assessment of cultural ecosystem services (Ruiz-Frau et al 2013)	CSIC	fisheries and non extractive marine species						marine ecosystems
Mapping outdoor recreationists' perceived social values for ecosystem services at Hinchinbrook Island National Park, Australia	CSIC							Wetlands, coral reefs

(van Riper et al 2012)								
Temporal variability in the benthos: Does the sea floor function differently over time? (Frid 2011)	CSIC	several invertebrate benthic species					arbitrary scales for body size, longevity, bioturbation, water depth categories, feeding mode	benthic macrofauna community

Appendix 1 - Table 2b - Part 1 - Marine Model Applications

Model name	Partner	Model Category	Ecosystem service (CICES terminology)	Brief description of model logics
Coastal protection (Liquete et al 2013)	CSIC	Spatial proxy-based	coastal protection	Provides a conceptual and methodological approach to assess coastal protection as an ecosystem service at different spatial-temporal scales, and applies it to the entire EU coastal zone. The assessment of coastal protection incorporates 14 biophysical and socio-economic variables from both terrestrial and marine datasets. Those variables define three indicators: coastal protection capacity, coastal exposure and human demand for protection. The three indicators are then framed into the ecosystem services cascade model to estimate how coastal ecosystems provide protection, in particular describing the service function, flow and benefit.
InVEST Scenic quality provision (Guerry et al 2012)	CSIC	Spatial proxy-based	Cultural (aesthetic)	The InVEST scenic quality model allows users to determine the locations from which new nearshore or offshore features can be seen. It generates viewshed maps that can be used to identify the visual footprint of new offshore development. Inputs to the viewshed model include: topography and bathymetry, locations of offshore facilities of interest, and the locations of viewers (e.g. population centers or areas of interest such as parks or trails).
InVEST Marine carbon storage & sequestration (Guerry et al 2012)	CSIC	Spatial proxy-based	Carbon storage & sequestration	The marine carbon model estimates how much carbon is stored in coastal vegetation, how much carbon is sequestered in the sediments and the economic value of storage and sequestration.
InVEST Coastal protection (Guerry et al 2012)	CSIC	Spatial proxy-based	coastal protection	The InVEST Coastal Protection model quantifies the protective services provided by natural habitats of nearshore environments in terms of avoided erosion and flood mitigation. The model's profile generator prepares a 1D bathymetry transect of a shoreline, providing information about its backshore and the location of natural habitats. The transect is used to estimate the total water level and shoreline erosion in the presence and absence of nearshore marine habitats

InVEST Food provision (Guerry et al 2012)	CSIC	Spatial proxy-based	Food provision	InVESt model estimates the quantity and monetary value of fish haversted by commercial fisheries. Appropiate to use for single species or groups of species with similar life stories. It estimates annual production of fish. Another section of the model can be used to analyse the production and monetary value of farmed fish and shellfish and quantify by-products of farming.
InVEST Marine renewable energy (Guerry et al 2012)	CSIC	Spatial proxy-based	Energy	Models energy production from waves an models off-shore wind energy production. The model asseses potential wave power and energy based on wave conditions and technology-specific ccapabilities.
InVEST Recreation (Guerry et al 2012)	CSIC	Spatial proxy-based	Recreation	The InVEST recreation model predicts the spread of person-days of recreation, based on the locations of natural habitats and other features that factor into people's decisions about where to recreate
Spatial PREdiction of benthic HABitats in the Baltic Sea (PREHAB) (Lindegarth et al 2014)	CSIC	Spatial proxy-based	Food provision	Predictive mapping of species distributions; it integrates human pressures into ecological and economic assessments.
Spatially explicit economic assessment of cultural ecosystem services (Ruiz-Frau et al 2013)	CSIC	Spatial proxy-based	Recreation, Food provision	This study presents an assessment of the economic importance and spatial distribution of non-extractive uses of marine biodiversity (diving, kayaking, wildlife watching from boats and seabird watching) in the coastal temperate area of Wales and its application to MSP.

Mapping outdoor recreationists' perceived social values for ecosystem services at Hinchinbrook Island National Park, Australia (van Riper et al 2012)	CSIC	Spatial proxy-based	Recreation and Aesthetic qualities	This model analyzes on-site and mailback survey data (n = 209) using the Social Values for Ecosystem Services (SolVES) GIS application to incorporate measures of social value and natural resource conditions on Hinchinbrook Island National Park, Australia.s
hydrodynamic model (Temmerman et al 2012)	CSIC	Phenomenological	Mediation of flows (flood protection)	Hydrodynamic model simulations of flood attenuation by a tidal marsh, with particular focus on the effects of spatial patterns of vegetation dieoff. Tidal marsh die-off, which may increase with ongoing global change (e.g. because sea level rise), is expected to have non-linear effects on reduced coastal protection against flood waves.
hydrodynamic model (Shepherd et al 2007)	CSIC	Phenomenological	Maintenance of physical, chemical and biological conditions (nutrient removal and carbon sequestration)	Hydrodynamic model to estimate nutrient removal and carbon sequestration in a UK estuary covered with tidal wetlands and mudflats, based on sediment dynamics and composition. The model also estimates the associated value of habitat created under a scenario of extensive managed realignment. A cost benefit analysis of the managed realignment is conducted too.
mangrove's wind protection (Das et al, 2013)	CSIC	Phenomenological	Mediation of flows (wind protection)	Modelation of wind attenuation and protection offered by mangroves in the event of wind-related damange during storms, specially in areas affected by tangential wind

InVEST (Guerry et al 2012)	CSIC	Phenomenological	multiple ES (renewable energies, food from fisheries and aquaculture, coastal protection, aesthetic, recreation and carbon storage and sequestration.	InVEST tool maps, quantifies, and values the services provided by seascapes. The tool is a flexible and scientifically grounded set of computer based models that focuses on ES (derived from the underlying biophysical processes that produce them); is spacially explicit, provides outputs in both biophysical and monetary and non monetary value terms; is scenario driven; clearly reveals relationships among multiple services and has a modular tiered approach to accommodate a range of data availability and the state of system knowledge. Designed to be integrated with stakeholder engagement processes.
Ecosim/EcoPath (Alcamo 2005)	CSIC	Macroecological	Provisioning, nutrition, biomass (fish production)	Fish production (landings) is estimated for three regional fisheries (Guf of Thailand, Central North Pacific North Benguela) for 4 different scenarios. The model computes dynamic changes in selected marine ecosystems as a function of fishing efforts (Pauly et al. 2000). For its fish production estimates, the EcoSim/EcoPath model takes into account not only the future source of feed for aquaculture, but also future subsidies for the fishing industry, the management objectives of fishing (either to optimize employment or profits), and the impact of climate change on shifts in species distribution and abundance (Pauly et al. 2003). For all scenarios, fish catch (by weight) is maintained in the North Benguela fishery, not maintained in the Central North Pacific, and has mixed results in the Gulf of Thailand. The overall message of these results is that it is uncertain whether future demands for fish can be sustainably provided by either aquaculture or marine fisheries.
Multiscale ecological and economic models salmon, shrimp & blue crab (Jordan et al 2012)	CSIC	Macroecological	Provisioning, nutrition, biomass (food production)	Model of the link between the production functions of critical habitats to commercial and recreational fishery values through the combination of specific research data with spatial analysis and population models

CO2 capture potential of seagrass restoration (Duarte et al, 2013)	CSIC	Trait-based	Maintenance of physical, chemical and biological conditions (carbon sequestration)	Model of the long term carbon sequestration expected for seagrass restoration programmes
Role of eelgrass in ES, food web modeling (Plummer et al 2013)	CSIC	Trait-based	multiple ES (provisioning, cultural, supporting)	Use of dynamic simulations in a food web model of central Puget Sound, Washington, USA developed in the Ecopath with Ecosim software, to examine how the marine com- munity may respond to changes in coverage of native eelgrass (Zostera marina), and how these modeled re- sponses can be assessed using an ecosystem services framework, expressing these services with economic currencies in some cases and biological proxies in others.
Temporal variability in the benthos: Does the sea floor function differently over time? (Frid 2011)	CSIC	Trait-based	Food provision, carbon cycling and nutrient regeneration	This paper examines decadal shifts of species composition in two stations in the Baltic and assesses how they alter provision of ‘ecosystem goods and services’
Mercury sequestration (Anastacio et al 2013)	CSIC	Process-based	Mediation of waste, toxics and other nuisances	Modelling of growth and mercury (HG) sequestration by Bolboschoenus maritimus on the most contaminated area of a temperate shallow coastal lagoon historically subjected to heavy Hg load, under gradients of climate driven variables. Simulation of B. maritimus mercury sequestration under different environmental scenarios involving increases and decreases in temperature, salinity and cloud cover. The largest effects were related to high salinity scenarios but all variables presented an inverse relation with Hg-sequestration
Barbier 2012	CSIC	NA	mediation of flows (storm protection) & fish density	Modelling of ecological production functions that decline across a coastal landscape

bioeconomic model (Sanchirico and Springborn 2011)	CSIC	NA	Provisioning, nutrition, biomass (fish production)	Bioeconomic model of a coral reef-mangrove-seagrass system to analyze the dynamic path of incentives to achieve an efficient transition to the steady state levels of fish biomass and mangrove habitat conservation.
Ecological-economic model (Leslie et al, 2009)	CSIC	NA	Provisioning, nutrition, biomass (Fisheries)	Analyses the impacts of multiple economic sectors on the marine ecosystem and dependent human community in the Gulf of California

Appendix 1 - Table 2b - Part 2 - Marine Model Applications

Model name	Partner	Main strengths	Limitations	Existing applications (other than OPERAs)	Use in Examplars (cite examplar)	Literature reference(s)
Coastal protection (Liquete et al 2013)	CSIC					Liquete et al, 2013. Ecological indicators, 30: 205-217
InVEST Scenic quality provision (Guerry et al 2012)	CSIC		The model does not quantify economic impacts of altering the viewshed, but it can be adapted to compute viewshed metrics for use in a more detailed valuation study. A key limitation of the model is that it does not currently account for the ways in which vegetation or land-based infrastructure may constrain land areas that are visually affected by offshore development.			Guerry et al, 2012. International journal of biodiversity science, ecosystem services and management, 8(1-2): 107-121
InVEST Marine carbon storage & sequestration (Guerry et al 2012)	CSIC					Guerry et al, 2012. International journal of biodiversity science, ecosystem services and management, 8(1-2): 107-121

InVEST Coastal protection (Guerry et al 2012)	CSIC	A primary limitation is that the Erosion Protection model assumes that all erosion leads to a loss of land. Further, the model estimates coastal protection services provided by habitats in terms of the reduction in damages due to erosion from storm waves, not surge. Some coastal habitats have the ability to attenuate surge in addition to waves (e.g., marshes, coastal forests), while other nearshore subtidal habitats do not (e.g., eelgrass). the model has technical limitations. The first is the lack of high quality GIS data that are readily available. The theoretical limitations of the Nearshore Waves and Erosion model are more substantial. As mentioned earlier, wave evolution is modeled with a 1D model. This assumes that the bathymetry is longshore-uniform (i.e. the profile in front of the site is similar along the entirety of the stretch of shoreline). Because this is unlikely true, the model ignores any complex wave transformations that occur offshore of the site of interest		Guerry et al, 2012. International journal of biodiversity science, ecosystem services and management, 8(1-2): 107-121
InVEST Food provision (Guerry et al 2012)	CSIC	It does not model behaviour , for that reeason it is not well suited to the evaluation of how human uses may change in response to changes in the marine environment.		Guerry et al, 2012. International journal of biodiversity science, ecosystem services and management, 8(1-2): 107-121

InVEST Marine renewable energy (Guerry et al 2012)	CSIC				Guerry et al, 2012. International journal of biodiversity science, ecosystem services and management, 8(1-2): 107-121
InVEST Recreation (Guerry et al 2012)	CSIC		The model does not presuppose that any predictor variable has an effect on visitation. Instead, the tool estimates the magnitude of each predictor's effect based on its spatial correspondence with current visitation in the area of interest. It requires the assumption that people's responses to attributes that serve as predictors in the model will not change over time. In other words, in the future, people will continue to be drawn to or repelled by the attributes as they are currently.		Guerry et al, 2012. International journal of biodiversity science, ecosystem services and management, 8(1-2): 107-121
Spatial PREdiction of benthic HABitats in the Baltic Sea (PREHAB) (Lindegarth et al 2014)	CSIC				Lindegarth, et al. 2014. Testing the Potential for Predictive Modeling and Mapping and Extending Its Use as a Tool for Evaluating Management Scenarios and Economic Valuation in the Baltic Sea (PREHAB). AMBIO , 43:82–93

Spatially explicit economic assessment of cultural ecosystem services (Ruiz-Frau et al 2013)	CSIC		Ruiz-Frau et al 2013. Spatially explicit economic assessment of cultural ecosystem services: Non-extractive recreational uses of the coastal environment related to marine biodiversity. Marine Policy 30: 90–98
Mapping outdoor recreationists' perceived social values for ecosystem services at Hinchinbrook Island National Park, Australia (van Riper et al 2012)	CSIC		van Riper et al 2012. Mapping outdoor recreationists' perceived social values for ecosystem services at Hinchinbrook Island National Park, Australia. Applied Geography 35: 164e173
hydrodynamic model (Temmerman et al 2012)	CSIC		Temmerman et al 2012. Global and Planetary Change 92–93; 267–274
hydrodynamic model (Shepherd et al 2007)	CSIC		Shepherd et al 2007. Estuarine, Coastal and Shelf Science 73 (2007) 355-367

mangrove's wind protection (Das et al, 2013)	CSIC	The study found that not accounting for the role of mangroves significantly overestimates actual wind damage. Wind barriers like mangroves reduces tangential wind and contributes subtantially to reduce wind-caused damage to structures	While the simplicity of the model makes it very tractable for use in empirical studies in poor regions, further model development and better data would shed more light on the particular mechanisms underlying mangrove protection from storms	Das et al 2013. Estuarine and coastal shelf science, 134, 98-107
InVEST (Guerry et al 2012)	CSIC	The multiple ES nature of InVEST helps expand the scope of planning conversation from single-issue perspectives to more comprenhensive discussions about cumulative impacts and benefits.		Guerry et al, 2012. International journal of biodiversity science, ecosystem services and management, 8(1-2): 107-121
Ecosim/EcoPath (Alcamo 2005)	CSIC	Global application	not stated	Alcamo, J; van Vuuren, D; Ringler, C; Cramer, W; Masui, T; Alder, J; Schulze, K. 2005. Ecology and Society, 10 (2)

Multiscale ecological and economic models salmon, shrimp & blue crab (Jordan et al 2012)	CSIC	Ecological production functions generally are observed at fine spatial scales for brief spans of time, whereas the resulting ecosystem services and their economic values may be delivered over broad geographic and temporal scales. This paper demonstrates methods of modeling and estimation that link fishery production and its associated economic indicators to the distributions and attributes of coastal habitats across scales ranging from habitat patches to large ocean basins.			Jordan et al 2012. Marine and coastal fisheries, 4(1):573-586
CO2 capture potential of seagrass restoration (Duarte et al, 2013)	CSIC	The model indicates that the cumulative C sequestered increases rapidly over time and with planting density. The value corresponding to this C sequestration suggests that the costs of seagrass restoration projects may be fully recovered by the total CO2 captured in societies with a carbon tax in place	The model presented delivers rough, but conservative, estimates of the average CO2 capture capacity associated with seagrass restoration projects. These estimates are con- servative because they focus on the mean, whereas plant- ing of seagrass patches for CO2 capture can be managed to achieve maximum capture, which could double the esti- mates provided above. In addition, the model considers clonal spread alone, whereas the restored meadows would produce seeds as they develop, contributing to accelerate colonization beyond the limits imposed by clonal growth, accelerating space occupation and therefore carbon capture.		Duarte et al 2013. Journal of Applied Ecology, 50, 1341-1349

Role of eelgrass in ES, food web modeling (Plummer et al 2013)	CSIC	Increased eelgrass coverage was most associated with increases in commercial and recreational fishing with some small decreases in one non-market activity, bird watching. When ES categories were considered (aggregations of individual groups of species) there was little evidence of strong tradeoffs among marine resources; that is, increasing eelgrass coverage was essentially either positive or neutral for all services examined			Plummer et al 2013, Ecosystems 16: 237-251
Temporal variability in the benthos: Does the sea floor function differently over time? (Frid 2011)	CSIC				Frid 2011. Temporal variability in the benthos: Does the sea floor function differently over time? Journal of Experimental Marine Biology and Ecology 400: 99–107
Mercury sequestration (Anastacio et al 2013)	CSIC	tool to analyze system behavior and to make projections regarding mercury sequestration. This is particularly relevant in the case of human interventions (i.e. engineering) for the optimization of this ecosystem service	the value calculated does not include sequestration by other plants sharing the habitat with B. maritimus. For this reason we should expect that the total value for mercury sequestration by wetland plants will be higher since other plant species are present in the studied area		Anastacio et al. 2013. Ecological Modelling 256, 31-42

Barbier 2012	CSIC	The basic model demonstrates how spatial production of ecosystem services affects the location and extent of landscape conversion. An extension allows for the risk of ecological collapse, when the critical size of the remaining landscape that precipitates the collapse is not known. Both models are simulated using the example of spatial variation in ecosystem services across a mangrove habitat that might be converted to shrimp aquaculture.			Barbier 2012, Ecological Economics 78, 70-79
bioeconomic model (Sanchirico and Springborn 2011)	CSIC				Sanchirico and Springborn 2011. Environ Resource Econ, 48:243–267
Ecological-economic model (Leslie et al, 2009)	CSIC	Three aspects of the findings are of particular interest: the clear trade- offs among the sectors and services we modeled; the influence of the typology of the socialÐecological link- ages (i.e., how ecosystems, services, and human com- munities are connected); and the influence of varying magnitude of the socialÐecological linkages.	It focused on a single fish species. the model would be strengthened by the collection of further empirical information specific to the social and ecological systems of the Gulf of California. Information on the economic costs and benefits of exploiting nearshore marine fish populations (as well as other elements of this ecosystem) and effort dynamics would be particularly informative, as would data on the social networks, mobility, and preferences of the fishermen, tourists and other key ac- tors. Investigation of how changes in		Leslie et al, 2009. Ecological research, 24:505-519

	functional forms, e.g., the relationships between catch and artisanal and sportsfishing effort, influence the ecological and social dynamics of our model systems, would be beneficial as well.	