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Review

Pathways to bridge the biophysical realism gap in ecosystem services mapping approaches

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ABSTRACT

The mapping of ecosystem service supply has become quite common in ecosystem service assessment practice for terrestrial ecosystems, but land cover remains the most common indicator for ecosystems ability to deliver ecosystem services. For marine ecosystems, practice is even less advanced, with a clear deficit in spatially-explicit assessments of ecosystem service supply. This situation, which generates considerable uncertainty in the assessment of ecosystems' ability to support current and future human well-being, contrasts with increasing understanding of the role of terrestrial and marine biodiversity for ecosystem functioning and thereby for ecosystem services. This paper provides a synthesis of available approaches, models and tools, and data sources, that are able to better link ecosystem service mapping to current understanding of the role of ecosystem service providing organisms and land/seascape structure in ecosystem functioning. Based on a review of literature, models and associated geo-referenced metrics are classified according to the way in which land or marine use, ecological processes and especially biodiversity effects are represented. We distinguish five types of models: proxy-based, phenomenological, niche-based, trait-based and full-process. Examples from each model type are presented and data requirements considered. Our synthesis demonstrates that the current understanding of the role of biota in ecosystem services can effectively be incorporated into mapping approaches and opens avenues for further model development using hybrid approaches tailored to available resources. We end by discussing ways to resolve sources of uncertainty associated with model representation of biotic processes and with data availability.

Contents

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1. Introduction

Ecosystem services (ES) originate from spatially structured ecosystems and land/seascapes, and their dynamics over time. Quantifying ES provisioning therefore must account for spatio-temporal patterns and processes. Although this is evident, so far this challenge has been insufficiently resolved (Bennett et al., 2015). Spatially-explicit quantification of ES using geo-referenced metrics and GIS-based approaches has recently gained prominence through the needs from policy and decision-makers for global to local ES assessments (Maes et al., 2012; Martinez-Harms et al., 2015). Similar needs follow from emerging practices of land and marine planning (Outeiro et al., 2015; von Haaren and 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 incorporate ecosystem services among use allocation and management criteria.

However the reliability of ES mapping varies as a function of the methods employed. For instance in a review of 107 studies, Lautenbach et al. (2015) found that, while half of ecosystem service studies were based on relatively simple look-up table approaches attributing fixed values for given land cover types, nearly a third of the studies of ecosystem services conducted between 1966 and 2013 mapped ecosystem services. This mapping is done in most cases based on land use composition ignoring land use configuration and land use intensity (Lautenbach et al., 2015; Mitchell et al., 2015; Verhagen et al., 2016). More specifically, regulating services have been the most commonly mapped, followed by provisioning services (Egoh et al., 2012; Lautenbach et al., 2015; Martinez-Harms and Balvanera, 2012; Seppelt et al., 2011). For marine and coastal systems, among a total of 27 available studies from an exhaustive search of the Web of Science on ES mapping and ES modelling studies, almost half (52%) focused on Regulation & Maintenance services, of those 22% concentrated on coastal protection (wind & flood protection) and 33% on carbon sequestration and storage. A further third of the studies (33%) focused on provisioning services, particularly on food production (i.e. fish). The rest of the studies (19%) mapped cultural services.

Linked with this increased practice of mapping ES provisioning, several recent reviews have summarised available methods used to map ES. In the following we refer to 'models' as quantitative representations of ES variables depending on abiotic, biotic and social parameters. Overall, statistical models quantifying ES supply based on relationships with biophysical and social variables are prevalent, while process models based on causal relations are still rare (Crossman et al., 2013; Egoh et al., 2012; Lautenbach et al., 2015; Martinez-Harms and Balvanera, 2012). For terrestrial ecosystems, static maps of land use and land cover are the most commonly used indicator for ES in Europe (Egoh et al., 2012) and the second most common globally (Martinez-Harms and Balvanera, 2012). This widespread application of methods with weak links to ecosystem processes leads to severe uncertainty in the mapped ES supply from national (Eigenbrod et al., 2010) to landscape (Lavorel et al., 2011) scales. More advanced approaches incorporate estimates of above- and sometimes below-ground biomass, along with vegetation type, and soil parameters for the estimation of ecosystem functions from which services are derived. Species observation data, although potentially useful for the estimation of cultural services, is used only rarely. Contrasting with these statistical models, process models, with explicit description of causal relationships between driver variables and ecosystem functions and properties underpinning ES provision, have primarily been used to map climate regulation and erosion control as well as the provisioning of food, fuel and fibre. Mapping and modelling assessments for marine and coastal ES are still in their infancy (Liquete et al., 2013). Considering the 27 available studies from the Web of Science, 31% of the models were geostatistical while less than 20% were process-based.

Beyond the limitations of specific mapping methods, the large variety of primary indicators currently used to express one single ES is a large source of uncertainty for ES maps that limits their usefulness to managers and decision makers (Egoh et al., 2012). Level of process understanding, modelling methodology and data sources are three of the critical, yet poorly understood or documented sources of uncertainty for ES maps (Grêt-Regamey et al., 2014a; Hou et al., 2013; Kandziora et al., 2013). A systematic comparison of four sets of ecosystem service maps at the continental scale for five ecosystem services (climate regulation, flood regulation, erosion protection, pollination and recreation) showed considerable disagreement among spatial patterns across Europe (Schulp et al., 2014a), attributed to differences in the mapping aim, indicator definitions, input data and mapping approaches. The four original studies encompassed a land-cover look-up approach (Burkhard et al., 2012), environmental indicator modelling (Kienast et al., 2009) and two hybrid approaches combining environmental indicators, landscape effects and process modelling (Maes et al., 2012; Schulp et al., 2008; Stürck et al., 2014; Tucker et al., 2014; van Berkel and Verburg, 2011). In addition to highlighting the need for mapmakers to clearly justify the indicators used, the methods and related uncertainties, this study provided additional support for the urgent need for better process understanding and data acquisition for ES mapping, modelling and validation. Progress on these issues will be essential to support the uptake of ES spatial assessments for national ecosystem service assessments, national accounts, land planning and broader policy and natural resource management decisions (Crossman et al., 2013; Egoh et al., 2012).

Given this context, the common use of relatively simple statistical approaches contrasts with increasing evidence on the role of biodiversity for ecosystem functioning and ecosystem services (Cardinale et al., 2012), which has been referred to as a *lack of biophysical realism* (Seppelt et al., 2011). Ecosystem service supply is related to the presence, abundance, diversity and functional characteristics of service-providing organisms (also referred to as Ecosystem Service Providers, ESP henceforth; Luck et al., 2009). Positive relationships have been found between species richness and ecosystem services such as fodder and wood production, regulation of water quality through soil nutrient retention, carbon sequestration or regulation of pest and weed species (Cardinale et al., 2012). Similarly, the presence of key coastal and marine species has been found to enhance carbon sequestration, coastal protection, food provision or water quality through nutrient retention and particle trapping (Fourqurean et al., 2012; McLeod et al., 2011; Ondiviela et al., 2014; van Zanten et al., 2014). However such observed relationships between species richness and ES often reflect species functional traits and their diversity within communities, rather than species richness per se (Diaz et al., 2007). Lastly, land/sea-scape diversity and connectivity can strongly influence the ES provided by mobile organisms and vegetation (Fahrig et al., 2011; Mellbrand et al., 2011; Mitchell et al., 2015). To provide more reliable estimates of service supply capacity by ecosystems, such fundamental ecological understanding needs to be better incorporated into ES models (Bennett et al., 2015).

This paper aims to address the biophysical realism gap in ecosystem service mapping by synthesising available approaches, models and tools, and data sources (with special reference to Europe) for mapping ecosystem services, and focusing on how the role of ecosystem service providing biota can be better incorporated. Based on a review of published mapping studies, modelling methods and associated geo-referenced metrics are classified into five categories according to the way in which the contribution of ecosystem service providing organisms is represented. This review highlights the diversity of individual methods, which increasingly combine different model categories. We end by discussing associated uncertainties and pathways towards resolving them. Our review focuses on assessment of ecosystem capacity to deliver services and does not address the social and economic aspects of ecosystem service demand.

2. Methods

We reviewed ES biophysical modelling approaches in the literature that incorporate descriptions of ecosystem service providers (ESP) and their contribution to ES supply. Given our objective of analysing the merits and limitations of available models rather than producing a quantitative analysis of the state of the art, for terrestrial systems we did not attempt to reiterate the several systematic reviews that have already been published (Lautenbach et al., 2015; Martinez-Harms and Balvanera, 2012; Seppelt et al., 2011), while for marine systems a systematic analysis of publications was conducted. As we aimed to assess how biophysical realism was incorporated in different approaches, we chose to classify models and associated geo-referenced metrics according to the way in which the relationships between ESP and biophysical processes are represented, using the following terminology: spatial proxy models, phenomenological models, niche-based models, trait-based models and full process-based models (Fig. 1). Briefly, spatial proxy models refer to simple models based on expert knowledge or statistical associations relating abiotic and biotic indicators to ES provision. Phenomenological models add to these by explicitly incorporating effects of land/seascape configuration through spatial processes. Niche-based models deduce ES provision from the geographic distribution of ESP, while trait-based models depict statistical relationships between ecosystem processes and indicators of ESP community functional composition. Lastly, we refer to full process-based models as those incorporating explicit representations of geochemical, physical and biotic processes underpinning ecosystem functioning.

For each category of models we describe and exemplify based on published studies (supported by standard model descriptions presented in Appendix A) the principles and mechanics of application of these models, with specific reference to how ESP are represented. Main biodiversity components for ESP characterisation and the strengths and weaknesses of different model types for practice are summarised in Table 1. Table 2 summarises main data sources for each model type, with specific reference to Europe for terrestrial (Table 2a) and marine (Table 2b) systems respectively. Lastly, key data sources and strengths and weaknesses for practice are discussed.

3. Results

3.1. Proxy models

We define proxy models as models that relate ES indicators to land or marine cover, abiotic and possibly biotic variables by way of calibrated empirical relationships or expert knowledge. It is desirable, and in practice most common for such models to use selected proxy variables that are based on well-known causal relationships between environmental variables (Kienast et al., 2009; Martinez-Harms and Balvanera, 2012). In proxy models habitat type (or biotope) or (more rarely) species composition are considered as the ESP. Most commonly land cover types, ranging from coarse vegetation types (e.g. evergreen vs. deciduous forest) to detailed habitat types such as those of the European Union's Habitats Directive, are associated with levels of ES supply, with the possible incorporation of additional environmental modifiers (e.g. altitude, soil type, climate. . .). 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.

One simple, and often used method consists in combining look-up tables allocating ES values per land cover with modifying categorical variables describing abiotic factors and ecological integrity (Burkhard et al., 2012). For example, in the Austrian Stubai valley, Schirpke et al. (2013) combined maps of vegetation types with measures of ES to map past, current or future fodder quantity and quality, carbon sequestration, soil stability, natural hazard regulation and aesthetic value. In 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. In marine ecosystems, bathymetry, habitat distribution, sediment type, wave and currents regime, tidal range and water temperature are most frequently used proxies. Liquete et al. (2013) developed a proxy-based model to assess coastal protection at European level based on 14 biophysical and socioeconomic variables describing coastal protection capacity, coastal exposure and demand for protection. Statistical models developed from observations or analysis of regional data sets may also be applied. Multiple regression models, Generalized Additive Models (Yee and Mitchell, 1991) or more sophisticated methods for capturing uncertainty in relationships, such as Bayesian modelling (Grêt-Regamey et al., 2013) may be used here. In general, the application of models developed at larger scale to smaller extents and greater resolution generates uncer-

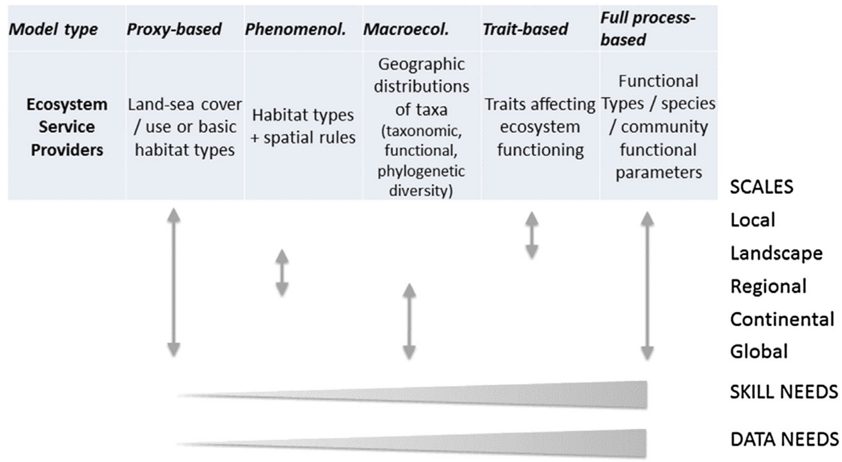

Fig. 1. Biodiversity components incorporated into different categories of models of ecosystem service supply.

tainty as they do not capture context-dependent relationships (Purtauf et al., 2005) and the effects of finer-grained relevant variables such as soils. Site-specific models may be developed based on field data collection (as encouraged by Martinez-Harms and Balvanera, 2012–see Lavorel et al., 2011) and on remote sensing data (Table 2, Fig. 2). On the other hand, the validity of up-scaling from site-specific models to larger spatial scales depends on whether sites represent the average conditions at the larger scale. It has further been shown by Grêt-Regamey et al. (2014b) that spatially explicit information about non-clustered, isolated ES tends to be lost at coarse resolution, mainly in less rugged terrain, which calls for finer resolution assessments in such contexts.

In the marine case, proxy models have generally been used to map the distribution of coastal vegetation such as mangrove coverage, which then has been used to estimate carbon sequestration and storage. In contrast, proxy models have had a limited application for the assessment of "underwater" marine ES, and we contend that this mainly reflects the limitations of remote sensing for correctly determining underwater habitat coverage.

3.1.1. *Strengths and weaknesses for practice*

Sophisticated proxy 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) and allow consistent mapping of different ecosystem services, which is essential for avoiding data artefacts when studying trade-offs. Model applications are however constrained by the availability of different data layers depending on scales and regions. For instance, while effects of soil parameters on regulation services (e.g. carbon sequestration, erosion control) are well understood by scientists and practitioners, soil maps are often not available at suitably fine resolution.

3.2. *Phenomenological models*

Phenomenological models are based on qualitative or semi-quantitative relationships between ESP and ES supply, based on an understanding of biological mechanisms underpinning ES supply. In difference to simple proxy models, at least part of the parameters and relationships are transferred from in-depth process-based studies or *meta*-analyses of observations. They assume, but do not represent explicitly, a mechanistic relationship between elements of the landscape, considered as ESP units, and the provisioning of ES. This often implies considering landscape configuration explicitly, contrary to simple land cover proxy models. This relationship might be represented by a functional relationship between landscape attributes and services, or might also incorporate spatial configuration. For example, the ES supply of a forest patch might depend on land cover, patch size and additional attributes such as soil quality or topography. However, quantitative biodiversity indicators are not commonly used in this type of models that are often dominated by the influence of land cover/use, although biodiversity indicators might be used, e.g. by incorporating a statistical relationship between plant or bird species richness and recreational value of a location. 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.

Phenomenological approaches have been applied for ecosystem services provided by mobile organisms and ecosystem services relating to lateral flows for which consideration of spatial configuration is essential (Mitchell et al., 2015; Verhagen et al., 2016). As a simple example of mobile ESP, 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). Phenomenological approaches that incorporate landscape configuration are commonly used to model pollination through the interplay between habitats suitable for wild pollinators and demand from insect-pollinated crops (Grêt-Regamey et al., 2014a; Lautenbach et al., 2011; Maes et al., 2011; Schulp et al., 2014b). Based on a *meta*-analysis by Ricketts et al. (2008) these models represent realised pollination as a decay function based on the distance between pollinator habitat and fields with pollination-dependent crops. The InvESt pollination model (Lonsdorf et al., 2009) includes the location of crops to be pollinated and the habitat quality for different pollinator species or guilds, as well as the availability of floral resources. More sophisticated versions also limit the number of cells that can be pollinated by pollinator source (Lautenbach et al., 2011), and Grêt-Regamey et al. (2014a) used knock-off thresholds based on connectivity to modulate habitat quality.

The assessment of water quality regulation and recreation by Lautenbach et al. (2011), and the universal soil loss equation (USLE) and related approaches (Wischmeier and Smith, 1978) for the quantification of erosion control (Schirpke et al., 2013) represent

Table 1
Strengths and weaknesses of different model types for practice. Maes tiers refer to levels of model complexity (Grêt-Regamey et al., 2015). Criteria were rated according to expert opinion and synthesis of published studies.

Model type	MAES Tier	Ecosystem Service Provider representation	Scales	Skill needs	Data needs	Validation	Transferability in space and time
Proxy	1	Land cover/use or vegetation type	All	Low Tools: GIS application	Low-medium	Rare	Large uncertainty if local or past/future conditions exceed those of model development and validation
Phenomenological	2	Landscape pattern and processes	Mainly Local-regional	Low Tools: GIS application	Low-medium	Rare	Large uncertainty if local or past/future conditions exceed those of model development and validation
Niche-based	2–3	Species geographic distributions	Regional – continental	Medium Tools: Maxent (Elith et al., 2011), BIOMOD (Thuiller et al., 2009)	Medium Constrained by availability of modelled species distribution or of species distribution data.	Well developed	Designed for scenario projections Current limitations: lack species interactions, demographic and evolutionary processes
Trait-based	3	Trait effects on ecosystem functioning, and possibly spatial trait distributions	Local – regional Extension to continental scale through remote sensing	Medium-High Lack of readily available (or validated) models. Standardized packages for calculation of trait-based indices (Casanoves et al., 2011; Laliberté and Shipley, 2011).	Medium-High Constrained by availability of trait data and environmental layers (e.g. soils)	Easy but requires local data collection	Well-adapted for scenario projections. Risk of exceeding conditions/parameter space of model development and validation
Full process – large scale	3	Plant Functional Types Also possibly: individual species, traits	Regional – continental – global	High Tools: Complex computer models	High Long-term climate data, information on land use/cover change and N input	Well developed using spatial databases derived from remote sensing observations or from sampling	Designed for scenario projections Risk of exceeding conditions/parameter space of model development and validation
Full process – local-landscape scale	3	Plant Functional Types to individual species	Local – landscape – regional	High Tools: Complex computer models	High Long-term climate data, information on land use/cover change and N input	Well developed using spatial databases derived from remote sensing observations or from sampling	Depending on data availability

examples of commonly used phenomenological approaches for ES depending on lateral flows.

In the marine environment phenomenological models have been rarely used, however Townsend et al. (2014) developed a method whereby services were defined from a series of principles based on ecosystem functioning and linked to marine biophysical parameters to develop ES maps for an area in New Zealand (Fig. 3). Other studies have used phenomenological models to link the coverage of key habitats and their level of connectivity to fisheries production (Yee et al., 2014).

3.2.1. Strengths and weaknesses for practice

Phenomenological approaches depend on the validity of the qualitative or semi-quantitative relationships underlying the model. Typically, the required parameters are transferred from other study sites or obtained through *meta*-analysis. Results should

Table 2
(a) Data sources for parameterisation of different types of ecosystem service mapping methods, with specific reference to Europe. (a) Terrestrial ecosystems.

Model type	Primary data sources for Europe	Remote sensing data
Proxy	Land cover maps Vegetation data bases (Chytrý et al., 2011). European Vegetation Archive (EVA) Global Index of Vegetation-Plot Databases (http://www.givd.info) (Dengler et al., 2011) Potential lack of data layers (e.g. soils))	Mapping thematic variables like Land Use/Land Cover, Vegetation, Forest, Wetland, Water, Burnt area, etc. Regional scale (for mapping landscape units), medium spatial resolution data like multitemporal MODIS, Spot Vegetation or MeteoSat data to follow vegetation dynamic. Local scale (for mapping precise thematic variables): high spatial resolution Landsat8 or Sentinelle-2 (for passive RS data), RadarSat or TerraSar (for active RS data). (Ayanu et al., 2012 Burkhard et al., 2012; Kuenzer et al., 2014 Pettorelli et al., 2014)
Phenomenological	Maps or proxy of landscape elements (van der Zanden et al., 2013) Topographic information including Digital Elevation Models: road networks, river networks (Lehner and Döll, 2004), coastlines (USGS HYDRO1 K, 2015) Biophysical data including soil data (European Soil database see Panagos et al., 2012)	As for proxy models
Niche-based	Occurrence data for all European terrestrial vertebrate species: 187 mammals (Mitchell-Jones et al., 1999), 445 breeding birds (Hagemeijer et al., 1997), and 149 amphibians and reptiles (Gasc, 2004). Refined data for 275 mammals, 429 birds and 102 amphibians across the Palearctic at 300 m resolution by incorporating 46 GlobCover land use/land cover classes(Maiorano et al., 2013). Clustering at 10′ by (Zupan et al., 2014). Extensive distribution data available for 1280 higher plants; digitized Atlas Flora Europeae. Trees: exhaustive data at 1 km^2 resolution (http://www.efi.int/portal/virtual_library/information_services/mapping_services/tree_species_maps_for_european_forests/). More comprehensive species distribution data available on a country per country basis, and for specific regions within a same country. Availability of phylogenies currently increasing, especially in Europe. Mega-phylogenies for higher plants, mammals and birds for Europe (Thuiller et al., 2011), with further complements for the Palearctic and amphibians by (Zupan et al., 2014). Trait data for functional diversity: see trait-based models	Texture variables like object size and shape, compactness, homogeneity/heterogeneity, neighborhood relationships, fragmentation, connectivity, relevant for plant type specification and habitats characterization. Global scale, Meteosat or SpotVegetation. Regional scale, medium spatial resolution data like multitemporal MODIS; can characterize vegetation dynamics. (Ayanu et al., 2012; Burkhard et al., 2012; Kuenzer et al., 2014; Pettorelli et al., 2014)
Trait-based	Community composition data – locally measured or from vegetation data bases as for proxy-based models. There are currently no public community composition data bases for animals Site-level measurements following standard methods (Cornelissen et al., 2003). Communal plant trait data bases, e.g. TRY (Kattge et al., 2011). 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 available for many species globally. Traits requiring more time-consuming, expensive, or technically-demanding measurements, and especially root traits poorly available. Trait data bases for birds (Pearman et al., 2014), mammals (PanTHERIA (Jones et al., 2009)), amphibians (http://amphibiaweb.org/), fish (FishBase (Froese and Pauly, 2016)), phytoplankton (Litchman and Klausmeier, 2008), lotic invertebrates (Nicole et al., 2006), soil invertebrates (e.g. (Salmon et al., 2014) for Collembola).	Plant/Canopy height using laser scanning (LiDAR). Leaf phenology: satellite multi-temporal data or timelaps cameras (class by spatial resolution from coarse to fine): AVHRR NDVI time series, MODIS, Sentinelle-2, RadarSat-2, Pleiades; or aerial photos/hyperspectral data using airborne sensor. Using Radiative Transfer Models (RTM), leaf mass per area (for Specific Leaf Area SLA estimation), leaf water content using RTM and/or SWIR wavelengths of RS data (for leaf dry matter content), chlorophyll content (for leaf nitrogen concentration estimation). Methods operational at individual/population/community/ecosystem scales depending on RS data source. (Homolová et al, 2013; Kuenzer et al., 2014)
Full process – large-scale	Climate forcing from observations (e.g. Mitchell and Jones, 2005; Rudolf et al., 2010; Weedon et al., 2011) or from a suite of climate models (e.g. CMIP5, Taylor et al., 2012) Atmospheric CO_2 concentration from observations for the past and models for the future RCPs (e.g. Keeling et al., 2009). Land-use data historical reconstructions and future scenarios (e.g., Fader et al., 2010, 2015, Hurtt et al., 2011; Kaplan et al., 2012, Klein Goldewijk et al., 2011, 2010; Ramankutty and Foley 1999). Highly generalized classes of soil texture (e.g. by FAO/IIASA/ISRIC/ISSCAS/JRC, 2012). Drainage direction map (e.g. Döll and Lehner, 2002) for models that apply a river routine scheme allowing for studying ecosystem services related to water flows Global N deposition (e.g. Lamarque et al., 2010, 2011) and N fertilization of croplands (e.g. by Zaehle et al., 2011) for models accounting for C—N interations Population density maps (Klein Goldewijk, 2005; Klein Goldewijk et al. 2010) when this is required by fire disturbance modelling Communal plant trait data bases for PFT parameterisation, e.g. TRY (Kattge et al., 2011).	1) RS data provide model inputs, 2) RS data for calibrating model parameters, 3) RS data for evaluation of models output. Models that are run for scenario studies obviously must be prognostic models that are not fed by RS data. Frequent terrestrial indicators that are derived from RS data are e.g. Land use/Land cover, topography, phenology, gross primary production, evapotranspiration, but see the reviews in Turner et al. (2004), Andrew et al. (2014). At the global scale, the often used satellite instruments are Landsat, Meteosat, Spot-Vegetation, NOAA-AVHRR, ATSR, MISR, SeaWiFS (e.g. Ayanu et al., 2012, Kelley et al., 2013, Randerson et al., 2009). Remote Sensing derived land use data (e.g. Hansen et al., 2013 for forest extent, loss, and gain from 2000 to 2012) are typical model inputs. Seasonal fraction of absorbed photosynthetically active radiation (fPAR) can be used as input by process-models (Potter et al., 1993), but they are also useful tools for the validation of full process-models that simulate the fPAR based on the modelling of biophysical processes (Bondeau et al., 2007; Lindeskog et al., 2013).

Table 2 (*Continued*)

Model type	Primary data sources for Europe	Remote sensing data
Full process – local-landscape-scale	Input data (historical and scenarios) as for large-scale process-based models with the additional possibility for local-landscape scale data Climate forcing from observations (e.g. UKCP09) Land-use/land management data: Fuchs et al., 2013, CORINE land cover (EEA, 2012), Salmon-Monviola et al., 2012 Detailed DEM and soil quality maps (Krysanova et al., 2005)	The same distinction as above between remote-sensing data for model input data or for model calibration/validation can be made. For vegetation mapping (like thematic variables) at the local or very local scale use of RS satellite data at 1 to 5 m spatial resolution (Worldview, Pleiades, Spot 6–7, Rapid-Eye, Quickbird, . . .). For vegetation and soil characterization (plant diversity, heterogeneity, soil roughness, compaction, etc.), use of airborne RS data like NIR aerial photos, hyperspectral data or full-waveform LiDAR. (Feng et al., 2010)

(b) Data sources for parameterisation of different types of ecosystem service mapping methods, with specific reference to Europe. (b) Marine ecosystems.

Model type	Primary data sources for Europe	Remote sensing data
Proxy	– Data on 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 (Liquete et al., 2013) – Data on fishing fleet and fishing grounds distribution, value of landings, harvest rate information, price of harvested products (Guerry et al., 2012) – Data on stored C, rate of C accumulation in sediments, market and non-market valuation of C (Guerry et al., 2012)	LandSat images from US Geological Survey Landsat (Shapiro et al., 2015) EU Corinne Land Cover (Liquete et al., 2013) Modelled seabed habitat maps (Liquete et al., 2013) ALOS AVNIR-2 (Advanced Land Observation Satellite Advanced Visible and Near Infrared Radiometer type 2) (Wicaksono et al., 2016)
Phenomenological	– Sediment and bathymetry charts, point source contaminant data, tidal model outputs, seabed shear stress and expert information (Townsend et al., 2014)	
Niche-based	– WorldClim Bioclim data (Jardine and Siikamaeki, 2014) – Fisheries landings, effort data, habitat GIS coverages, survival rates for habitat types, salinity (Jordan et al., 2012)	
Trait-based	– Seagrass patch growth, parch survival in seagrass planting projects, estimates of seagrass CO_2 sequestration per unit area (Duarte et al., 2013)	
Full process – large-scale	– Submarine habitat cover (Yee et al., 2014)	
Full process – local-landscape-scale	– Use of biogeochemical model; Dissolved Organic Carbon; Particulated Organic Carbon; nutrients; carbonates; zooplankton; microzooplankton; phytoplankton (Canu et al., 2015)	

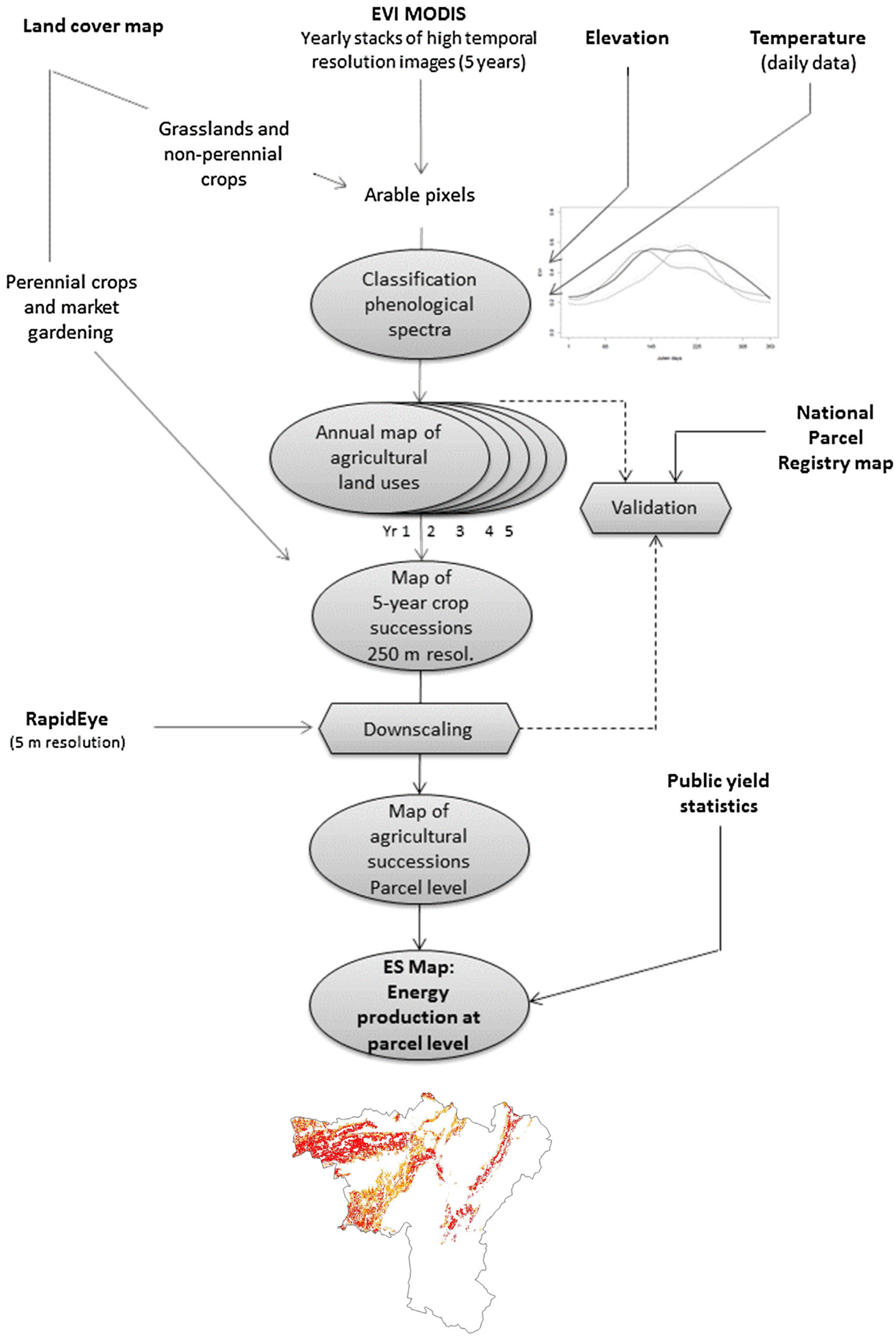

Fig. 2. Proxy-based spatial modelling of five-year average crop production (energy equivalent MG/ha) (2008–2012) for the Grenoble urban area (France). Schematic method identifying crop succession over 5 years at parcel scale using MODIS data for determining winter/spring crops based on phenology of photosynthetically active biomass. Adapted from Lasseur et al. in review.

therefore be interpreted as indicators of the direction or spatial variation of an effect or of the relative importance of an effect (e.g. by comparing different land use scenarios or historic land use data) rather than absolute values. The strength of the approach it incor-

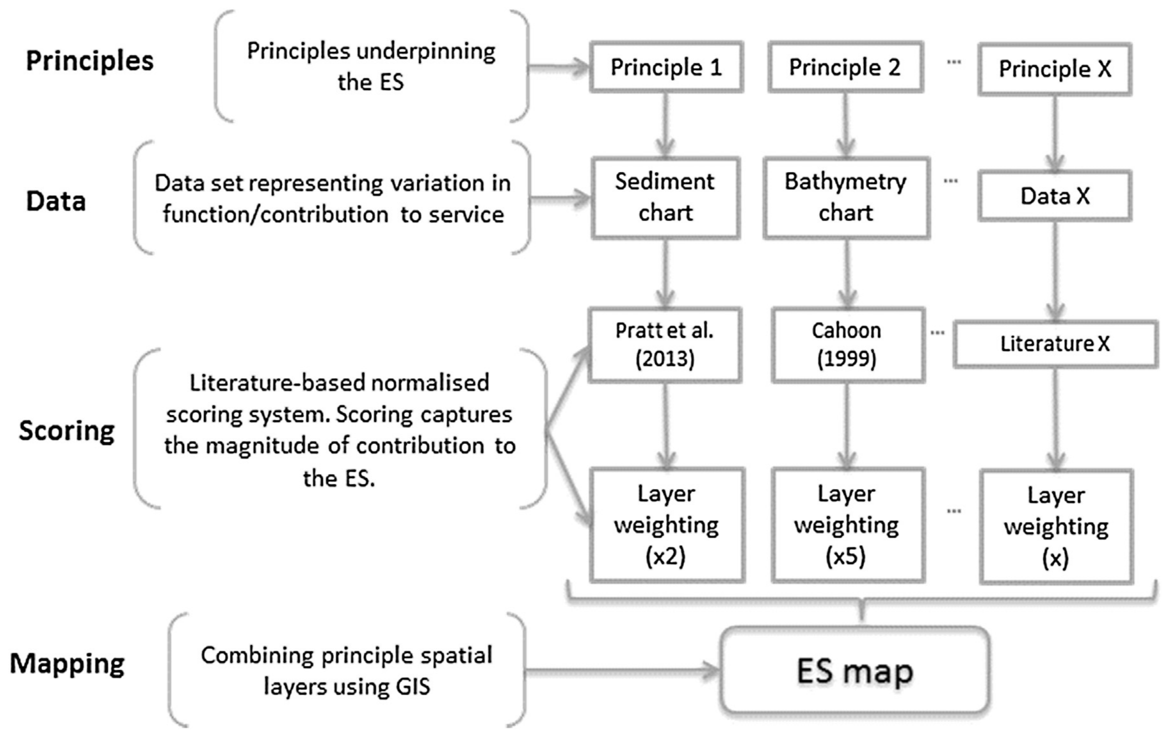

Fig. 3. Phenomenological model development for mapping marine ecosystem services based marine ecological principles. Adapted from Townsend et al., 2014.

porates land use configuration effects while requiring only limited data. It can therefore be used to get first estimates at scales where data availability is limited, such as the regional scale, or for the assessment of past conditions for which required data for more sophisticated approaches will not become available.

3.3. Niche-based models

We define as niche-based models of ES models that assess ES supply based on the presence (or abundance) of ESP (often species) depending on their geographic distribution (Fig. 4). ES can be modelled by aggregating distribution maps for different ESP if there are more than one contributing species, thus considering for instance the number of ESP species as a proxy for ES supply. A frequent limitation to such an approach is the lack of continuous distribution maps of ESP occurrence. To overcome this, Species Distribution Modelling (SDM) (Elith and Leathwick, 2009; Guisan and Thuiller, 2005) can be used to produce statistical relationships that predict the probability of occurrence of a given species (or group of species) over geographic areas 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 full 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 animal behaviour. 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.

Niche-based models may in particular apply to cultural services provided by well-identified species (e.g. protected species, species of particular aesthetic value) or to provisioning services by particular species such as in the case of wild foods (Schulp et al., 2014c). In Mediterranean regions provisioning services such as timber, fuelwood or cork production can be related to the presence of particular species (e.g. *Fagus sylvatica* or *Quercus ilex*, or *Quercus suber* respectively) and to forest species richness (Vilà et al., 2007; von Essen, 2015), 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* (Lloret et al., 2003). Niche-based modelling was applied to model biocontrol of vertebrate and invertebrate pests by terrestrial vertebrates (birds, mammals, reptiles) in Europe, considering predator species richness as a proxy for biocontrol potential (Civantos et al., 2012). As SDMs enable the projection of ESP distribution under changing environmental conditions, this approach showed that under future climate change scenarios pest control would be substantially reduced, especially in southern European countries, whereas in much of central and northern Europe climate change would likely to benefit pest-control providers. In coastal and marine environments niche-based models have been primarily used to model the distribution of mangroves and thus their carbon capture and storage capacity (Hutchison et al., 2014; Sunny and Juha, 2014) and fisheries production, based on species distribution models (Jordan et al., 2012).

In principle, any method of aggregation is possible, although so far species richness for ESP (i.e. added contributing species) has been considered as the proxy for ES without applying any weighting to different species. Though in their infancy, approaches considering relationships between taxonomic, phylogenetic and functional diversity and their links to ES (Flynn et al., 2011) are good candidates to expand existing ones. These approaches build on the premise that since functional diversity, or functional composition tend to be better related to ES supply than species richness or diversity (Cardinale et al., 2012), then niche-based models of species distributions could be translated to 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 ES (Cadotte et al., 2009).

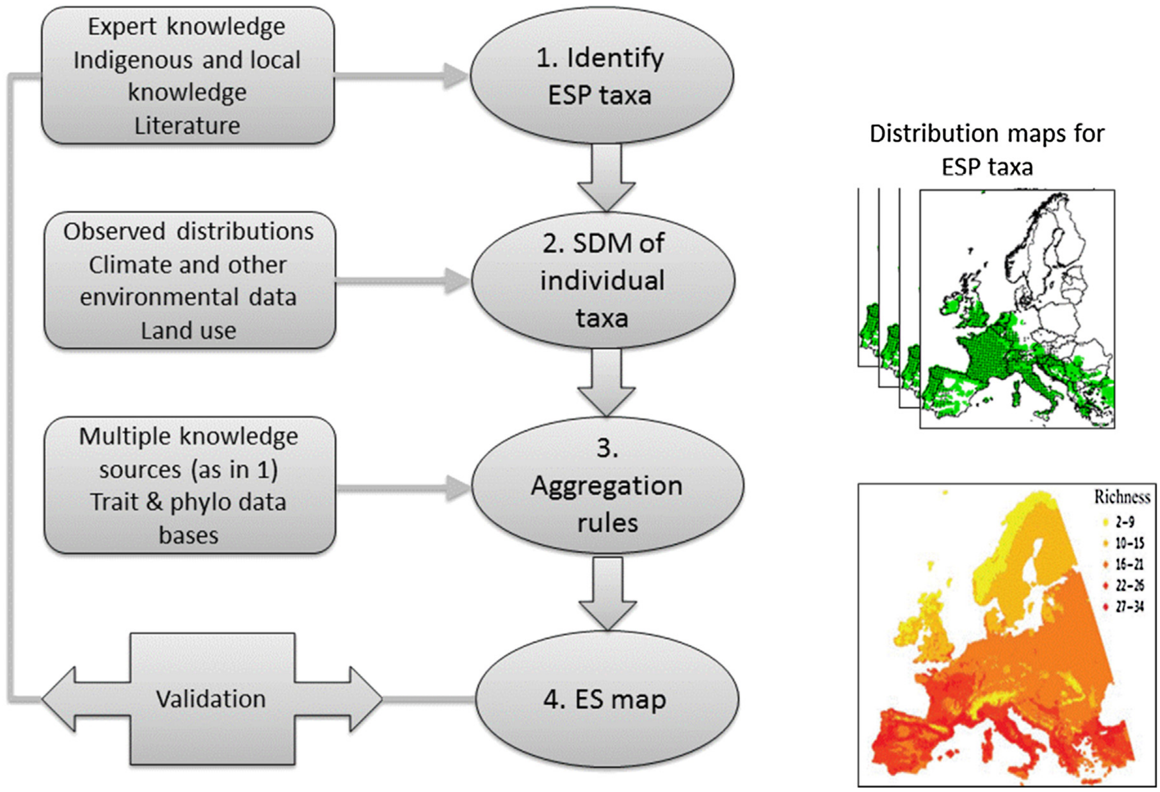

Fig. 4. Macro-ecological models of ecosystem service supply potential. ESP: ecosystem service provider; SDM: species distribution modelling. Here the final map uses richness of vertrebrate predators of rodents as an indicator for potential capacity to control rodents in Europe (from Civantos et al., 2012).

3.3.1. *Strengths and weaknesses for practice*

Overall, niche-based modelling of species distributions is a well-developed approach with free accessible tools, suitable for future scenario projections (.e.g BIOMOD: Thuiller et al., 2009; Maxent: Elith et al., 2011). Species distribution data are often the critical bottleneck for niche-based approaches. Limitations of SDM and strengths and weaknesses of different distribution modelling methods have been discussed extensively (e.g. Bellard et al., 2012; Elith and Leathwick, 2009), and improvements proposed (Zurell et al., 2016). 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 ESP and ES supply. This gap requires both greater ecological understanding (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.

3.4. *Trait-based models*

There is increasing evidence for the relevance of traits of organisms as ES providers (De Bello et al., 2010; Lavorel, 2013; Luck et al., 2009). Trait-based models quantify ES supply based on 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 trait-based models reduce uncertainty in ES prediction over space as compared to models based on land use alone, or even land use and soil variables (Eigenbrod et al., 2010; Martinez-Harms and Balvanera, 2012). Such models are constructed based on empirical measures of ecosystem functioning, which are then related to explanatory variables including: land cover/use, trait-based metrics quantifying functional diversity of ESP (Mouchet et al., 2010), soil variables and, for regional to continental scale or topographically complex landscapes climate/microclimate variables. Models may combine metrics for several individual traits, e.g. plant height and leaf nitrogen concentration to model grassland productivity (Lavorel et al., 2011); or use multi-trait metrics such as a compound index of different traits, e.g. the leaf economics spectrum (Laliberté and Tylianakis, 2012; Lienin and Kleyer, 2012; Mokany et al., 2008) or multivariate trait diversity (e.g. Conti and 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, 2013). 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. Multitrophic trait-based models 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 and Stockan, 2013), herbivores (Ibanez et al., 2013), or soil microorganisms (de Vries et al., 2012; Legay et al., 2014), and their effects of ES supply (Grigulis et al., 2013; Moretti et al., 2013). In principle, and similar to niche-based models, a wide range of modelling methods are suitable, although selected methods must allow spatially-extensive extrapolation over space for which explanatory variables are available, and preferably across time under scenarios.

As an example, 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 (Fig. 5). These models were 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).

The initial construction of trait-based ES models requires observational or experimental data sets measuring ecosystem properties underpinning ES supply along with community composition of ESP. ESP community composition can then be combined with original, site-level trait data, or data extracted from trait data bases, but considering uncertainties resulting from intraspecific trait variability (Kazakou et al., 2013; Violle et al., 2012). Scenario projections can be parameterised by combining projected values for land use and environmental parameters with new community-level trait values calculated based on species compositional turnover from e.g. state-and-transition models (Quétier et al., 2007) and on intraspecific variability measured along environmental gradients (Albert et al., 2010) or through experiments (Jung et al., 2014).

Increasing trait data availability through communal data bases and remote sensing offers high promises for the development of trait-based models of ES (Table 2a). There are 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.

3.4.1. 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. Such models also provide a mechanistic basis for the understanding of biophysical bundles and trade-offs in ES supply (Lavorel and Grigulis, 2012; Mouillot et al., 2011). The existence of so called 'response – effects overlaps' (Lavorel and Garnier, 2002; Suding et al., 2008) enables 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. So far trait-based ES models have rarely been validated across sites, although inter-site analyses have identified generic trait-based models of fodder production, fodder digestibility and litter decomposability (Fortunel et al., 2009; Gardarin et al., 2014; Lavorel et al., 2013b), and the model by Gardarin et al. (2014) was applied to map fodder quality at national scale (Violle et al., 2015). Lastly, trait-based models will become increasingly attractive as trait data bases become more generally available, although the lack of soil data layers in many regions will remain problematic.

3.5. Full process-based models

Full process-based models of (terrestrial) ecosystems rely on the explicit representation, using mathematical formulations, of ecological, physical, and biogeochemical processes that determine the functioning of ecosystems. The predictive algorithms simulate a large range of variables, which can then be post-processed to quantify ES. Process-based models have been most widely applied to quantify i) climate regulation (Bayer et al., 2015; Duarte et al., 2013; Metzger et al., 2008; Naidoo et al., 2008; Ooba et al., 2012; Watanabe and Ortega, 2014), ii) water supply, water quality, flood and erosion regulation (Gedney et al., 2006; Lautenbach et al., 2012a, 2013; Logsdon and Chaubey, 2013), iii) food, fodder, and bioenergy provision (Bateman et al., 2013; Beringer et al., 2011; Lindeskog et al., 2013; Müller et al., 2014), iii) natural hazard regulation (Elkin et al., 2013), but also in the wider frame of habitat characterisation (Hickler et al., 2012; Huntingford et al., 2011). Here, we discriminate between large-scale and local to landscape scale process-based models.

Appendix A lists examples using Dynamic Vegetation Models (DVM) (LPJ-GUESS and LPJmL: Bondeau et al., 2007; Sibyll et al., 2013; Sitch et al., 2003; Smith et al., 2001), Earth System Models (ESM) (JULES and ORCHIDEE: Cox, 2001; Krinner et al., 2005; Zaehle and Friend, 2010), hydrological models (SWAT and others: Neitsch et al., 2005; Stürck et al., 2014), forest dynamic models (e.g. Elkin et al., 2013; Bugmann, 1996) and models for ecological restoration (e.g. Chen and Twilley, 1998; Duarte et al., 2013). Fig. 6 represents the typical steps of ES assessments with process-based models and possible mapping outputs.

3.5.1. Large-scale process models

Several large-scale process models have been used for ES quantification. Dynamic Vegetation Models (DVMs) and Earth System Models (ESMs) are large-scale models that provide functional representations of plant and ecosystem processes that are universal rather than specific to one biome or region (Prentice and Cowling, 2013). Hydrological models represent water-related processes within river catchments (Gudmundsson et al., 2012). Global models typically apply a spatial resolution of $0.5^{\circ} \times 0.5^{\circ}$, but can be run at finer resolution, or even ecosystem scale if the required drivers are available. In that case, model adjustment might be necessary (e.g. re-calibration, re-formulation to better account for important processes of the region). Applications of these models that include a representation of regional specific features are often designed for local to regional scale application, like forest dynamic models and crop models.

This type of models uses a set of process formulations for representing key biogeochemical and physical processes as a function of prevailing atmospheric CO_2 concentration, climate, soil characteristics and eventually land use and management or nutrient deposition. Vegetation is represented as a mixture of plant functional types (PFTs) or species that are distinct in terms of bioclimatic limits and ecological parameters (see Lavorel et al., 2007; Woodward and Cramer, 1996), simulated or prescribed. 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), possibly under a given management type. Soil profile is described using up to ten layers. Hydrological models consider also shallow and deep aquifer storages, and a river routing module simulates the discharge to the rivers network. "Fast" processes are modelled on a daily or sub-daily basis and include energy and gas exchange, photosynthesis, respiration and plant-soil water exchanges. Processes with seasonal dynamics such as plant phenology, growth and biomass allocation are implemented on a daily or monthly basis. Mortality, disturbance, management, are represented on an annual or sub-annual basis, eventually stochastically. By using a small number of PFTs which represent a low-dimensional continuum of plant trait combinations, process-based models generally underestimate the functional diversity of biota in favour of a manageable number of classes. Yet the rise of super computers allows to run DVMs with

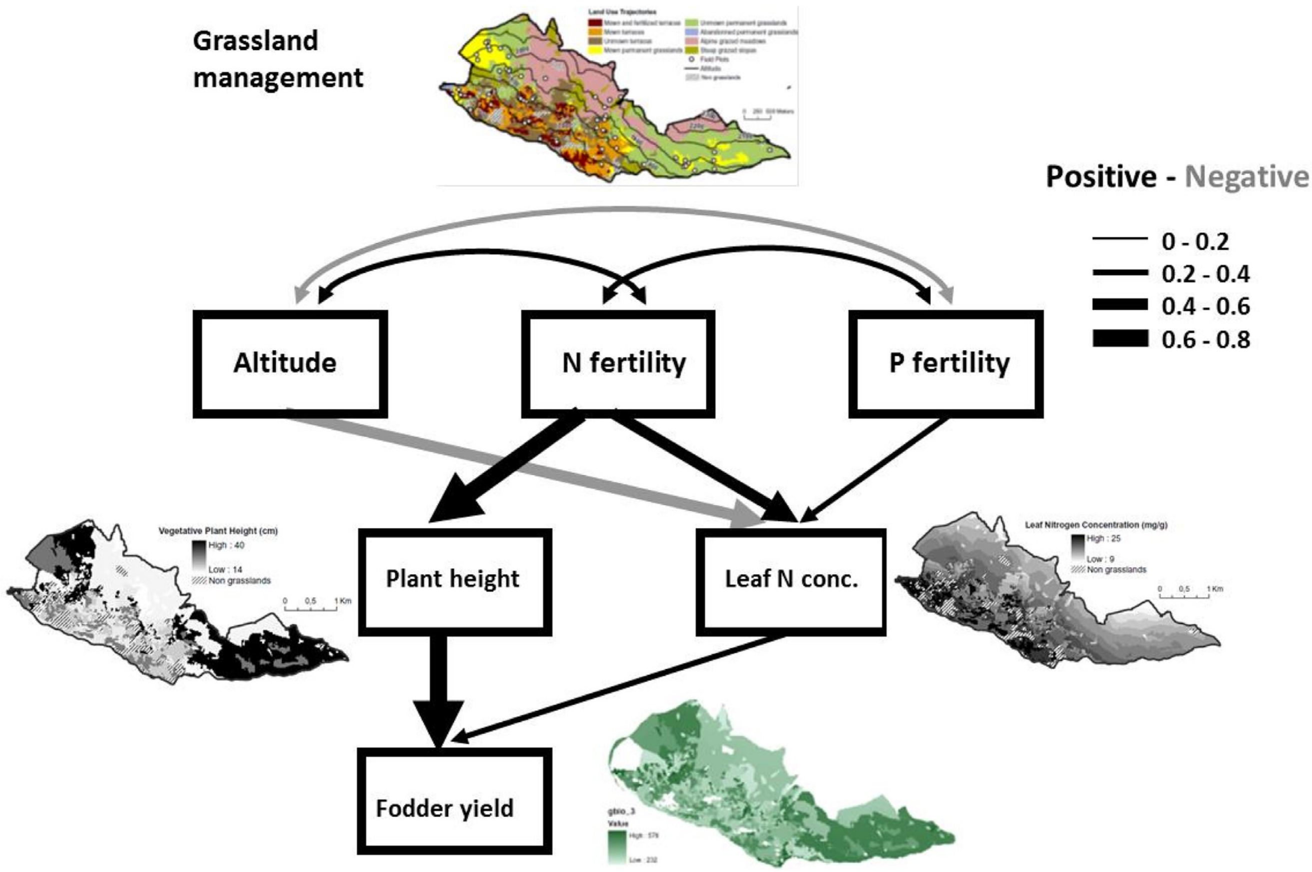

Fig. 5. Trait-based modelling of ecosystem service supply potential for mountain grasslands. Schematic summary of modelling steps based on cascading effects from land use and environmental variables, to community mean plant traits and to ES, illustrated here in the case of fodder production by mountain grasslands (adapted from (Lavorel et al., 2011) and (Lavorel and Grigulis, 2012)). N: nitrogen, P: phosphorus.

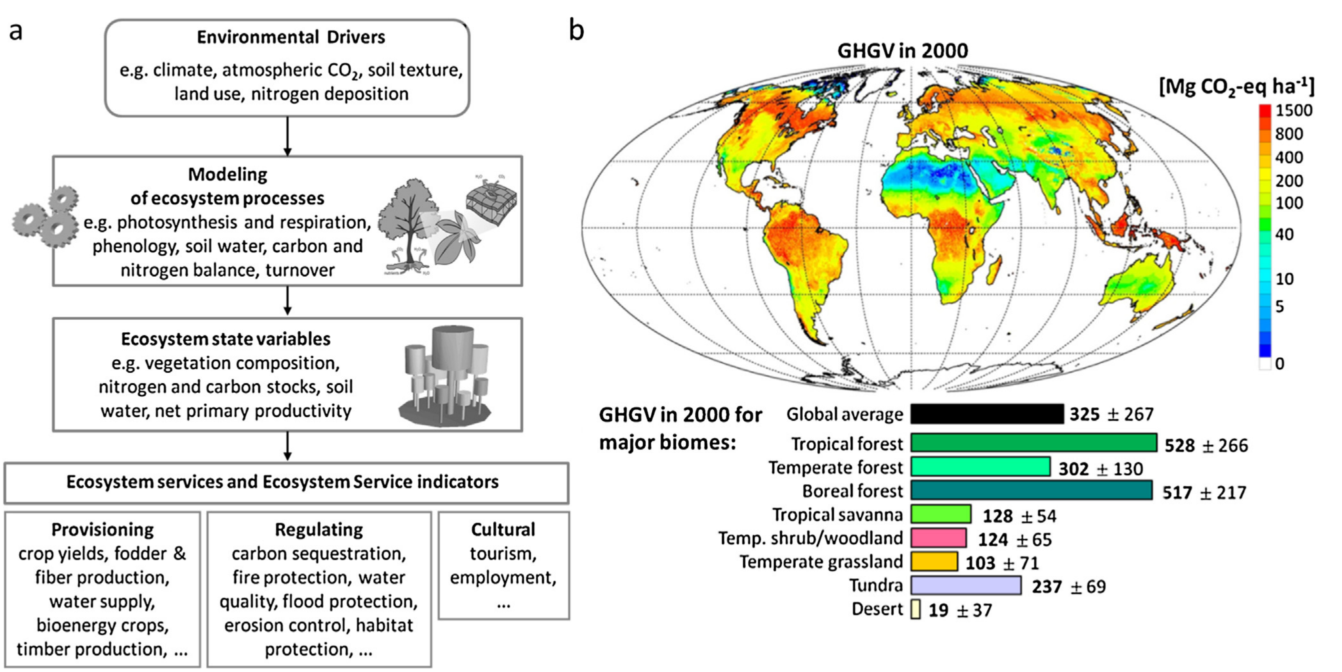

Fig. 6. Workflow typical for process-based models (a). Selected provisioning and regulating services are most often directly linked to simulated ecosystem state variables while cultural services may only derived from suitable indicators. Example application of a process-based model for the quantification of an ES metric accounting for the full biogeochemical implications of carbon sequestration by estimating contribution of CO_2 to the Greenhouse Gas Value (GHGV) (b) (Figure after Bayer et al., 2015).

flexible individual traits (Sakschewski et al., 2015), making it possible to account for functional diversity.

3.5.2. Local to landscape scale process models

At local to landscape scales, forest dynamic models with similar philosophy and structure as DVMs have been used for the assessment of bundles of ecosystem services including timber production, natural hazard regulation (avalanches, 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).

As another type of full-process models with strong potential for ES modelling, watershed models have been designed to simulate hydrological flows and often water quality at the landscape to regional scale. Soil infiltration, surface and subsurface flows as well as evapotranspiration and snowmelt are the main hydrological processes. For modelling water quality the transport and turnover of nutrients and other chemicals need to be represented as well as soil erosion processes, along with agricultural practices. Given the importance of vegetation for the water cycle a vegetation growth model is part of all watershed models. Specifically differences between different plants (or plant functional types) are considered for water use, and in nutrient use for crops. As an example, 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. The soil water assessment tool (SWAT) (Neitsch et al., 2005) is an example of an advanced watershed model applied to agricultural landscapes map water purification services (Lautenbach et al., 2012a), to assess fresh water provisioning, fuel provisioning, erosion regulation and flood regulation (Logsdon and Chaubey, 2013) and to describe trade-offs between food and fodder provisioning, biofuel provisioning, water quality regulation and discharge regulation (Lautenbach et al., 2013) depending on crop rotations and crop management.

For marine ecosystems, the Ecopath with Ecosim (EwE) modelling approach supports predictions of changes in fish to 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. At the core of EwE is Ecopath, a static, mass-balance snapshot of fisheries based on a set of linear equations combining net production that reflects the balance of catch, predation and other sources of mortality, migration, biomass accumulation, with respiration and unassimilated food., The Ecosim and Ecospace modules then build on this basic mass-balance module to simulate respectively temporal dynamics using differential equations, and spatial dynamics using spatially explicit distribution of habitat types and fishing effort, along with lateral movement. Alcamo et al. (2005) applied EwE to model fish consumption and production for three important regional marine fisheries (North Benguela, Central North Pacific and Gulf of Thailand) under the four Millennium Ecosystem Assessment global scenarios, showing that for all scenarios fish catch (by weight) was maintained in North Benguela, not maintained in the Central North Pacific, whereas results were scenario-sensitive in the Gulf of Thailand. Another process-based model is available for the long-term carbon sequestration expected from seagrass restoration programmes (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 enable the estimation of an optimal planting density to maximise C sequestration.

3.5.3. Strengths and weaknesses for practice

There is a substantially overlapping set of physiological and ecological principles that is used across process-based models to represent ecosystem dynamics and matter flows, providing robustness and scalability to these models for ES quantification. However, predictions of response variables, e.g. net primary productivity, vary considerably among individual large-scale models (e.g. Denman et al., 2007; Friedlingstein et al., 2006; Sitch et al., 2013). This is due to 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 and Cowling, 2013). Conversely, local and landscape scale process models can be limited by detailed parameterization and calibration needs and by availability of case-specific validation data.

Most process models have not been designed to model ecosystem services but to model the underlying ecosystem functions from which an ecosystem service is derived directly or indirectly. 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. Because they model processes and their fundamental biological and physical interactions they also appear particularly promising for exploring mechanisms underpinning synergies and trade-offs between ES (Viglizzo et al., 2016).

4. Discussion

Mobilising scientific understanding to assess the spatial distribution of ecosystem services is a tremendous challenge to support environmental assessment, planning and sustainable futures (Bennett et al., 2015; Maes et al., 2016). Because ES lie at the interface between social and environmental systems, this endeavour requires an integrated assessment of the social and ecological factors determining the production of ecosystem services (Reyers et al., 2013; Villamagna et al., 2013). In this review, we have focused solely on how the biophysical condition of ecosystems, as influenced by biotic, abiotic and management factors, determines ES supply, thus not considering ES demand, and how it influences ES flows and feedbacks to biophysical condition. Mapping ES demand is an even more challenging objective (Wolff et al., 2015), and will ultimately need to be coupled in integrated spatial ES assessments (e.g. Schulp et al., 2014b, 2014c; Stürck et al., 2014). In the following we discuss future avenues for further improvement of the mapping of ES supply by increasing biophysical realism, but this will need proceed along with parallel progress in accounting for ES demand.

4.1. Future avenues for increasing biophysical realism in ES mapping

Plant and Ryan (2013) identified the lack of an 'ES toolbox' as a barrier to the adoption of ES by natural resource managers. While this paper does not attempt to produce such a tool box, it provides a basis for guiding model choice by scientists and practitioners. Here, we identified two important dimensions which enable the incorporation of greater biophysical realism in models supporting ES mapping and can be developed into different model categories regardless of their baseline complexity. First, while simple land cover information is most commonly used to map ES, effects of land use configuration and land use intensity that can be captured by phenomenological models are too often ignored (Verhagen et al., 2016). Recent practice also shows the benefits of incorporating explicit land use rather than simple land cover information for the simplest proxy-based models all the way to advanced full process-based models Second, approaches incorporating explicitly the role of ES providing biota are emerging as powerful methods to reduce uncertainty in ES mapping. This includes models quantifying individual species effects, species diversity, functional traits, and ecosystem functions described in this review, and for which tools and data are becoming increasingly available. Our review also helps the selection of appropriate methods according to spatial scale, given that scale effects have so far been poorly considered in ES research (Grêt-Regamey et al., 2014b). Review of practice highlights (1) the predominant effect of scale on model selection for practical case studies, (2) the prospect within a single case study to combine different model types, of varying complexity and detail in the representation of biotic effects, depending on specific ES of interest, skills and data/resources availability.

The last point highlights that our categories of methods 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 (Grêt-Regamey et al., 2015), and especially a greater integration of explicit biodiversity effects 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. Stürck et al. (2014) used a hybridization between a process-based hydrological model and a spatial proxy, look-up approach to map flood regulation across Europe by determining the regulating capacity of different land use-soil combinations within a catchment. Schirpke et al. (2013) coupled the USLE phenomenological 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. Large scale full-process models are also evolving 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, recent models have started considering direct trait-based formulation (Scheiter and Higgins, 2009; Zaehle and 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 niche-based 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.

Quantifying and mapping marine ecosystem services has lagged behind efforts for terrestrial ecosystems, but this is in the process of changing (Liquete et al., 2013; Maes et al., 2012). Data and methods to assess the provision of services 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 is the lack of high-resolution spatial information for 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). However, efforts towards mapping marine habitats are increasing. In order to rapidly move towards biophysically realistic mapping, some large fundamental knowledge gaps regarding ecosystem processes need to be resolved. First, there is a lack of information at which scales ecosystem processes and functions occur and how these relate to the provisioning of services. Second, the relationships between biodiversity and ecosystem functions in marine ecosystems are still poorly known (Bergström et al., 2015; Moore et al., 2015). The literature search on marine models/mapping conducted as part of this review highlighted a considerable number of studies which stopped at the assessment or prediction of ESP distributions without taking the next step in analysing their implications for ES provision (e.g. Albouy et al., 2013; Bergström et al., 2015; Moore et al., 2015). Although this is not an easy problem, experience from terrestrial ecosystems in the integration of biotic processes and biodiversity effects into ES quantification and mapping may speed up progress for marine and coastal ecosystems.

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

While the importance of quantifying uncertainties and of model validation is accepted knowledge in the environmental and ecological modelling community (Bennett et al., 2012; Dormann et al., 2008; Jakeman et al., 2006; Laniak et al., 2013), these have been two enduring challenges for spatial explicit ES assessment (Crossman et al., 2013; Martinez-Harms and Balvanera, 2012; Seppelt et al., 2011).

Uncertainty can be conceptually separated into uncertainty about the model structure, uncertainty of model parameterization, uncertainty in the data and last but not least the conceptual uncertainty of the definition of an ecosystem service and underlying processes. In reality all these different components interact: data availability – especially at larger scales – drives in many situations the choice of proxys and the model structure for assessing an ES (Andrew et al., 2015). The use and parameterization of a model is limited by the availability of data – this can in turn lead to suboptimal decision about model structure which leads in turn to an increase in uncertainty. Choosing strongly simplified proxy-models to best match data availability may lead to ignoring the most important processes determining ecosystem service supply, and especially biotic processes. For ecosystem services that predominantly rely on mobile biota – such as pest control, or pollination – increased system understanding on how the different components of biodiversity affect ES provisioning of the services supports the development of more robust models suitable for spatial and temporal extrapolation (Kremen et al., 2007). At the same time, using the most advanced process models in the absence of data to parameterise them at the desired scale does not necessarily lead to higher accuracy. Still, incorporating at least phenomenological understanding into ES models would likely increase reliability and robustness of ES assessments and maps. The use of remote sensing data to estimate ecosystem service proxies (Ayanu et al., 2012; de Araujo Barbosa et al., 2015) and to derive information on biodiversity (O'Connor et al., 2015; Schmidtlein et al., 2012) (Table 2) is promising to overcome some of the data limitations, although the derivation of information from remote sensing data requires the use of additional models that bring in their own sources of uncertainty (Foody and Atkinson, 2002).

In the previous sections we have illustrated how better biodiversity process understanding can be incorporated to reduce uncertainty in ES models. The uncertainty introduced by a selected model structure can be assessed by comparing models of different structure, as recently done for species-distribution models (Buisson et al., 2009; Morin and Thuiller, 2009). Such comparisons can be used to highlight areas or situations in which models strongly agree or disagree. Schulp et al. (2014a) followed this approach by comparing ES maps from five distinct studies at the European scale, and such practice is now gaining currency to assess the value of novel model developments. Another strategy is the use of model ensembles for forecasts and assessments. This strategy which is common practice for full-process models is now spreading for niche-based and trait-based models (e.g. Araújo and New, 2007; Gritti et al., 2013; Thuiller et al., 2009).

As the availability on species, phylogenetic and functional biodiversity increases currently, along with remote sensing derived information, data availability is likely to become less limiting for using more advanced models (Table 2). But then uncertainty in biodiversity input data could propagate in ES models (Dong et al., 2015). Researchers will then need to estimate the effects of increasing model complexity both on feasibility of parameterisation and on sensitivity to uncertainty in the input data, and to carefully assess potential mismatches in temporal and spatial scale of the new data (Orth et al., 2015; Perrin et al., 2001). First, a specific source of uncertainty in ES assessment relates to the scale of the input data. Although the selection of the modelling scale should be driven by the requirements of the end user (the scale of the decision to be made) (Grêt-Regamey et al., 2014b), data availability seriously limits the degrees of freedom for the selection of input data. There should always be a match between the resolution for ESP biota and environmental data. This in particular applies to climate, where downscaled layers need to be available or calculated for adequate species distribution or process modelling. Conversely, care should also be taken in combining high resolution soil maps with biota data with a coarser resolution (Grêt-Regamey et al., 2014b). Second extrapolating models beyond the range of calibration data is a critical source of uncertainty. Black box statistical models, e.g. some phenomenological, niche-based or trait-based models that have been (over-)fitted to data without ensuring a robust model structure are especially prone to effects of extrapolation. In general, for an analysis of temporal changes or for assessing management options the projected effects should be compared to the sensitivity of the model outputs against reasonable parameter changes: if the direction of the effect changes or if the magnitude of the response is weaker than the sensitivity of the model one should hesitate to draw strong conclusions from the model. Examples for this approach can be found in Lautenbach et al. (2011) and Schulp et al. (2014b). It is also possible to test the sensitivity towards the uncertainty in the input data, an approach followed in Lautenbach et al. (2012b).

Thus, ES map users should be aware of the different sources of uncertainty and map creators should 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. If observed data is used for model parameterisation and calibration, it should be always possible to quantify the uncertainty attached. If no observed data is available against which model output could be compared sensitivity analysis is an option to quantify uncertainties. Lastly, validation of ES models is complicated by the fact that many ES cannot be directly measured. Water purification for example has to rely on water quality data not on measured purification rates (Lautenbach et al., 2012a). Therefore, model validation is often pattern-oriented, considering proxy-data, and tries to at least capture the system behaviour instead of specific process variables.

Ultimately, comparing the gains from improved biophysical process understanding to the possible propagation of uncertainties in biodiversity and ecosystem process data will determine the net benefits from using models of increasing biophysical complexity.

5. Conclusion

In order to achieve the ambitious political agenda for biodiversity, 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. We have summarised the main characteristics, strengths and weaknesses of different approaches for mapping ES supply, highlighting their complementarity depending on scale, assessment objectives and context, available skills and data. Review of practice 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 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.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2016.11.015.

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