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1 **Title: Pathways to bridge the biophysical realism**
2 **gap in ecosystem services mapping approaches**

3
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24

25

26 **Abstract**

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

47

48

49 **Keywords:** **Ecosystem Service Provider; spatial modelling; biophysical assessment;**
50 **species distribution; functional traits; large-scale ecosystem model**

51

52 1. Introduction

53 Ecosystem services (ES) originate from spatially structured ecosystems and land/seascapes,
54 and their dynamics over time. Quantifying ES provisioning therefore must account for spatio-
55 temporal patterns and processes. Although this is evident, so far this challenge has been
56 insufficiently resolved (Bennett et al., 2015). Spatially-explicit quantification of ES using geo-
57 referenced metrics and GIS-based approaches has recently gained prominence through the
58 needs from policy and decision-makers for global to local ES assessments (Maes et al.,
59 2012; Martinez-Harms et al., 2015). Similar needs follow from emerging practices of land and
60 marine planning (Outeiro et al., 2015; von Haaren and Albert, 2011) or land management
61 decision (e.g. in agriculture or forestry; Doré et al., 2011; Grêt-Regamey et al., 2013;
62 Soussana et al., 2012) that incorporate ecosystem services among use allocation and
63 management criteria.

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

80 Linked with this increased practice of mapping ES provisioning, several recent reviews have
81 summarised available methods used to map ES. In the following we refer to 'models' as
82 quantitative representations of ES variables depending on abiotic, biotic and social
83 parameters. Overall, statistical models quantifying ES supply based on relationships with
84 biophysical and social variables are prevalent, while process models based on causal
85 relations are still rare (Crossman et al., 2013; Egoh et al., 2012; Lautenbach et al., 2015;
86 Martinez-Harms and Balvanera, 2012). For terrestrial ecosystems, static maps of land use
87 and land cover are the most commonly used indicator for ES in Europe (Egoh et al., 2012)
88 and the second most common globally (Martinez-Harms and Balvanera, 2012). This
89 widespread application of methods with weak links to ecosystem processes leads to severe
90 uncertainty in the mapped ES supply from national (Eigenbrod et al., 2010) to landscape
91 (Lavorel et al., 2011) scales. More advanced approaches incorporate estimates of above-
92 and sometimes below-ground biomass, along with vegetation type, and soil parameters for
93 the estimation of ecosystem functions from which services are derived. Species observation
94 data, although potentially useful for the estimation of cultural services, is used only rarely.

95 Contrasting with these statistical models, process models, with explicit description of causal
96 relationships between driver variables and ecosystem functions and properties underpinning
97 ES provision, have primarily been used to map climate regulation and erosion control as well
98 as the provisioning of food, fuel and fibre. Mapping and modelling assessments for marine
99 and coastal ES are still in their infancy (Liquete et al 2013). Considering the 27 available
100 studies from the Web of Science, 31% of the models were geostatistical while less than 20%
101 were process-based.

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

123

124 Given this context, the common use of relatively simple statistical approaches contrasts with
125 increasing evidence on the role of biodiversity for ecosystem functioning and ecosystem
126 services (Cardinale et al., 2012), which has been referred to as a *lack of biophysical realism*
127 (Seppelt et al., 2011). Ecosystem service supply is related to the presence, abundance,
128 diversity and functional characteristics of service-providing organisms (also referred to as
129 Ecosystem Service Providers, ESP henceforth; Luck et al., 2009). Positive relationships have
130 been found between species richness and ecosystem services such as fodder and wood
131 production, regulation of water quality through soil nutrient retention, carbon sequestration or
132 regulation of pest and weed species (Cardinale et al., 2012). Similarly, the presence of key
133 coastal and marine species has been found to enhance carbon sequestration, coastal
134 protection, food provision or water quality through nutrient retention and particle trapping
135 (Fourqurean et al., 2012; McLeod et al., 2011; Ondiviela et al., 2014; van Zanten et al.,
136 2014). However such observed relationships between species richness and ES often reflect
137 species functional traits and their diversity within communities, rather than species richness
138 per se (Diaz et al., 2007). Lastly, land/sea-scape diversity and connectivity can strongly

139 influence the ES provided by mobile organisms and vegetation (Fahrig et al., 2011;
140 Mellbrand et al., 2011; Mitchell et al., 2015). To provide more reliable estimates of service
141 supply capacity by ecosystems, such fundamental ecological understanding needs to be
142 better incorporated into ES models (Bennett et al., 2015).

143

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

155

156

157 2. Methods

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

178 For each category of models we describe and exemplify based on published studies
179 (supported by standard model descriptions presented in Appendix 1 **Erreur ! Source du**
180 **renvoi introuvable.**) the principles and mechanics of application of these models, with

181 specific reference to how ESP are represented. Main biodiversity components for ESP
182 characterisation and the strengths and weaknesses of different model types for practice are
183 summarised in Table 1. Table 2 summarises main data sources for each model type, with
184 specific reference to Europe for terrestrial (Table 2a) and marine (Table 2b) systems
185 respectively. Lastly, key data sources and strengths and weaknesses for practice are
186 discussed.

187

188

189 **3. Results**

190

191 **3.1. Proxy models**

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

204 One simple, and often used method consists in combining look-up tables allocating ES
205 values per land cover with modifying categorical variables describing abiotic factors and
206 ecological integrity (Burkhard et al., 2012). For example, in the Austrian Stubai valley,
207 Schirpke et al. (2013) combined maps of vegetation types with measures of ES to map past,
208 current or future fodder quantity and quality, carbon sequestration, soil stability, natural
209 hazard regulation and aesthetic value. In traditional forest landscapes of Lapland, Vihervaara
210 et al. (2010) illustrated how multiple biophysical and social data sources can be combined to
211 quantify regulation service supply by different biotopes. In marine ecosystems, bathymetry,
212 habitat distribution, sediment type, wave and currents regime, tidal range and water
213 temperature are most frequently used proxies. Liqueste et al. (2013) developed a proxy-based
214 model to assess coastal protection at European level based on 14 biophysical and
215 socioeconomic variables describing coastal protection capacity, coastal exposure and
216 demand for protection. Statistical models developed from observations or analysis of regional
217 data sets may also be applied. Multiple regression models, Generalized Additive Models
218 (Yee and Mitchell, 1991) or more sophisticated methods for capturing uncertainty in
219 relationships, such as Bayesian modelling (Grêt-Regamey et al., 2013) may be used here. In
220 general, the application of models developed at larger scale to smaller extents and greater
221 resolution generates uncertainty as they do not capture context-dependent relationships

222 (Purtauf et al., 2005) and the effects of finer-grained relevant variables such as soils. Site-
223 specific models may be developed based on field data collection (as encouraged by
224 Martinez-Harms and Balvanera, 2012 – see Lavorel et al., 2011) [and on remote sensing data](#)
225 [\(Table 2, Figure 2\)](#). On the other hand, the validity of up-scaling from site-specific models to
226 larger spatial scales depends on whether sites represent the average conditions at the larger
227 scale. It has further been shown by Grêt-Regamey et al. (2014b) that spatially explicit
228 information about non-clustered, isolated ES tends to be lost at coarse resolution, mainly in
229 less rugged terrain, which calls for finer resolution assessments in such contexts.

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

235

236 **Strengths and weaknesses for practice**

237 Sophisticated proxy models have been recommended for national assessment of ecosystem
238 services (Maes et al., 2014). They help move from a pure ‘benefit transfer’ approach based
239 on land cover (Eigenbrod et al., 2010; MAES Tier 1), to more precise assessments (MAES
240 Tier 2) using classic GIS methods accessible to all (Kienast et al., 2009). Also, they can be
241 easily combined with socio-economic variables in order to provide at least first level
242 assessments of benefits (Burkhard et al., 2012; Grêt-Regamey et al., 2008; Vihervaara et al.,
243 2010) and allow consistent mapping of different ecosystem services, which is essential for
244 avoiding data artefacts when studying trade-offs. Model applications are however
245 constrained by the availability of different data layers depending on scales and regions. For
246 instance, while effects of soil parameters on regulation services (e.g. carbon sequestration,
247 erosion control) are well understood by scientists and practitioners, soil maps are often not
248 available at suitably fine resolution.

249

250

251 **3.2. Phenomenological models**

252 Phenomenological models are based on qualitative or semi-quantitative relationships
253 between ESP and ES supply, based on an understanding of biological mechanisms
254 underpinning ES supply. In difference to simple proxy models, at least part of the parameters
255 and relationships are transferred from in-depth process-based studies or meta-analyses of
256 observations. They assume, but do not represent explicitly, a mechanistic relationship
257 between elements of the landscape, considered as ESP units, and the provisioning of ES.
258 This often implies considering landscape configuration explicitly, contrary to simple land
259 cover proxy models. This relationship might be represented by a functional relationship
260 between landscape attributes and services, or might also incorporate spatial configuration.
261 For example, the ES supply of a forest patch might depend on land cover, patch size and
262 additional attributes such as soil quality or topography. However, quantitative biodiversity
263 indicators are not commonly used in this type of models that are often dominated by the

264 influence of land cover/use, although biodiversity indicators might be used, e.g. by
265 incorporating a statistical relationship between plant or bird species richness and recreational
266 value of a location. Typically, these approaches are used at the regional to the global scale
267 since the assumed relationships ignore most often smaller scale details and focus on
268 patterns emerging at coarser scales.

269 Phenomenological approaches have been applied for ecosystem services provided by
270 mobile organisms and ecosystem services relating to lateral flows [for which consideration of](#)
271 [spatial configuration is essential \(Mitchell et al., 2015; Verhagen et al., 2016\)](#). As a simple
272 example of mobile ESP, in the Swiss valley of Davos, the cultural service of habitat for the
273 protected bird species Capercaillie was modelled by combining habitat suitability criteria
274 relating to quality and spatial pattern with GIS-modelled vegetation distribution (Grêt-
275 Regamey et al., 2008). Phenomenological approaches that incorporate landscape
276 configuration are commonly used to model pollination through the interplay between habitats
277 suitable for wild pollinators and demand from insect-pollinated crops (Grêt-Regamey et al.,
278 2014a; Lautenbach et al., 2011; Maes et al., 2011; Schulp et al., 2014b). Based on a meta-
279 analysis by Ricketts et al. (2008) these models represent realized pollination as a decay
280 function based on the distance between pollinator habitat and fields with pollination-
281 dependent crops. The InvEST pollination model (Lonsdorf et al., 2009) includes the location
282 of crops to be pollinated and the habitat quality for different pollinator species or guilds, as
283 well as the availability of floral resources. More sophisticated versions also limit the number
284 of cells that can be pollinated by pollinator source (Lautenbach et al., 2011), and Grêt-
285 Regamey et al. (2014a) used knock-off thresholds based on connectivity to modulate habitat
286 quality.

287 The assessment of water quality regulation and recreation by Lautenbach et al. (2011), and
288 the universal soil loss equation (USLE) and related approaches (Wischmeier and Smith,
289 1978) for the quantification of erosion control (Schirpke et al., 2013) represent examples of
290 commonly used phenomenological approaches for ES depending on lateral flows.

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

297

298 **Strengths and weaknesses for practice**

299 Phenomenological approaches depend on the validity of the qualitative or semi-quantitative
300 relationships underlying the model. Typically, the required parameters are transferred from
301 other study sites or obtained through meta-analysis. Results should therefore be interpreted
302 as indicators of the direction or spatial variation of an effect or of the relative importance of
303 an effect (e.g. by comparing different land use scenarios or historic land use data) rather
304 than absolute values. The strength of the approach it incorporates land use configuration
305 effects while requiring only limited data. It can therefore be used to get first estimates at
306 scales where data availability is limited, such as the regional scale, or for the assessment of

307 past conditions for which required data for more sophisticated approaches will not become
308 available.

309

310 **3.3. Niche-based models**

311 We define as **niche-based** models of ES models that assess ES supply based on the
312 presence (or abundance) of ESP (often species) depending on their geographic distribution
313 (Figure 4). ES can be modelled by aggregating distribution maps for different ESP if there
314 are more than one contributing species, thus considering for instance the number of ESP
315 species as a proxy for ES supply. A frequent limitation to such an approach is the lack of
316 continuous distribution maps of ESP occurrence. To overcome this, Species Distribution
317 Modelling (SDM) (Elith and Leathwick, 2009; Guisan and Thuiller, 2005) can be used to
318 produce statistical relationships that predict the probability of occurrence of a given species
319 (or group of species) over geographic areas depending on parameters such as climate, soil
320 or land use, and generate continuous distribution maps of these taxa. There are also more
321 sophisticated, mechanistic models, which (akin to full process models – see below) model
322 species distributions based on physiological mechanisms (e.g. temperature tolerance
323 thresholds, temperature responses), phenology (the timing of specific life cycle events such
324 as bud burst or flowering in plants) or animal behaviour. The contribution of e.g. different
325 species or functional groups to the ES of interest is assessed based on specific traits (e.g.
326 trophic guilds) or expert knowledge.

327 **Niche-based** models may in particular apply to cultural services provided by well-identified
328 species (e.g. protected species, species of particular aesthetic value) or to provisioning
329 services by particular species such as in the case of wild foods (Schulp et al., 2014c). In
330 Mediterranean regions provisioning services such as timber, fuelwood or cork production can
331 be related to the presence of particular species (e.g. *Fagus sylvatica* or *Quercus ilex*, or
332 *Quercus suber* respectively) and to forest species richness (Vilà et al., 2007; von Essen,
333 2015), while spiritual and aesthetic values are supported by *Quercus suber* and *Pinus*
334 *halepensis*, and the regulation of fire hazards is promoted by *Quercus suber* but negatively
335 affected by *Pinus halepensis* (Lloret et al., 2003). **Niche-based** modelling was applied to
336 model biocontrol of vertebrate and invertebrate pests by terrestrial vertebrates (birds,
337 mammals, reptiles) in Europe, considering predator species richness as a proxy for
338 biocontrol potential (Civantos et al., 2012). As SDMs enable the projection of ESP
339 distribution under changing environmental conditions, this approach showed that under
340 future climate change scenarios pest control would be substantially reduced, especially in
341 southern European countries, whereas in much of central and northern Europe climate
342 change would likely to benefit pest-control providers. In coastal and marine environments
343 **niche-based** models have been primarily used to model the distribution of mangroves and
344 thus their carbon capture and storage capacity (Hutchison et al., 2014; Sunny and Juha,
345 2014) and fisheries production, based on species distribution models (Jordan et al., 2012).

346 In principle, any method of aggregation is possible, although so far species richness for ESP
347 (i.e. added contributing species) has been considered as the proxy for ES without applying
348 any weighting to different species. Though in their infancy, approaches considering
349 relationships between taxonomic, phylogenetic and functional diversity and their links to ES

350 (Flynn et al., 2011) are good candidates to expand existing ones. These approaches build on
351 the premise that since functional diversity, or functional composition tend to be better related
352 to ES supply than species richness or diversity (Cardinale et al., 2012), then [niche-based](#)
353 models of species distributions could be translated to functional diversity in order to generate
354 projections of ES. The incorporation of phylogenetic diversity, which can be easily computed
355 based on taxonomic data granted the availability of phylogenetic data (e.g. Thuiller et al.,
356 2011), adds a further means to approach functional diversity and thereby to quantify ES
357 (Cadotte et al., 2009).

358

359 [Strengths and weaknesses for practice](#)

360 Overall, [niche-based](#) modelling of species distributions is a well-developed approach with
361 free accessible tools, suitable for future scenario projections (.e.g BIOMOD: Thuiller et al.,
362 2009; Maxent: Elith et al., 2011). Species distribution data are often the critical bottleneck for
363 [niche-based](#) approaches. Limitations of SDM and strengths and weaknesses of different
364 distribution modelling methods have been discussed extensively (e.g. Bellard et al., 2012;
365 Elith and Leathwick, 2009), and improvements proposed (Zurell et al., 2016). Apart from the
366 intrinsic limitations of the approach, such as ignoring population dynamics, species
367 interactions, or potential adaptive responses, the main avenue for improvement towards the
368 application to ES modelling regards the understanding and quantitative specification of
369 relationships between ESP and ES supply. This gap requires both greater ecological
370 understanding (Cardinale et al., 2012; Nagendra et al., 2013), and research into the demand
371 for ES in terms of the identities and relative weights of contributing species.

372

373

374 **3.4. Trait-based models**

375 There is increasing evidence for the relevance of traits of organisms as ES providers (De
376 Bello et al., 2010; Lavorel, 2013; Luck et al., 2009). Trait-based models quantify ES supply
377 based on statistical, quantitative relationships between an ecosystem property underpinning
378 ES supply and trait-based metrics, as well as, if significant additional effects of abiotic
379 parameters such as climate or soil variables (Gardarin et al., 2014; Lavorel et al., 2011).
380 (Lavorel et al., 2011) demonstrated that trait-based models reduce uncertainty in ES
381 prediction over space as compared to models based on land use alone, or even land use
382 and soil variables (Eigenbrod et al., 2010; Martinez-Harms and Balvanera, 2012). Such
383 models are constructed based on empirical measures of ecosystem functioning, which are
384 then related to explanatory variables including: land cover/use, trait-based metrics
385 quantifying functional diversity of ESP (Mouchet et al., 2010), soil variables and, for regional
386 to continental scale or topographically complex landscapes climate / microclimate variables.
387 Models may combine metrics for several individual traits, e.g. plant height and leaf nitrogen
388 concentration to model grassland productivity (Lavorel et al., 2011); or use multi-trait metrics
389 such as a compound index of different traits, e.g. the leaf economics spectrum (Laliberté and
390 Tylianakis, 2012; Lienin and Kleyer, 2012; Mokany et al., 2008) or multivariate trait diversity
391 (e.g. Conti and Diaz, 2013; Mokany et al., 2008). A review of known relationships between

392 indicators of ecosystem biogeochemical functioning for plants, relevant to the modelling of
393 ES such as for instance fodder or timber production, climate regulation through carbon
394 sequestration or the maintenance of water quality, suggested that, for available studies so
395 far, community mean values of single traits tended to capture most of the variance in these
396 ecosystem properties (Lavorel, 2013). The recent extension to ES associated with other
397 biota such as soil fauna and microorganisms (Mulder et al., 2013), insects (Ibanez, 2012;
398 Moretti et al., 2013), terrestrial vertebrates (Luck et al., 2012), aquatic invertebrates
399 (Engelhardt, 2006) or marine fish (Albouy et al., 2013) holds high promises. Multitrophic trait-
400 based models quantify ecosystem services resulting from the interaction between several
401 trophic levels such as pollination, biotic control of pests and weeds or maintenance of soil
402 fertility (Grigulis et al., 2013; Lavorel et al., 2013a). These models capture not only the effects
403 of environmental change on ES via their effects on e.g. plant traits, but by also integrating the
404 traits that underpin biotic interactions between plants and other organisms such as
405 pollinators (Pakeman and Stockan, 2013), herbivores (Ibanez et al., 2013), or soil
406 microorganisms (de Vries et al., 2012; Legay et al., 2014), and their effects of ES supply
407 (Grigulis et al., 2013; Moretti et al., 2013). In principle, and similar to [niche-based](#) models, a
408 wide range of modelling methods are suitable, although selected methods must allow
409 spatially-extensive extrapolation over space for which explanatory variables are available,
410 and preferably across time under scenarios.

411 As an example, models of mountain grassland ES supply were developed based on plant
412 traits (Lavorel et al., 2011), and further complemented by traits of soil microorganisms
413 (Grigulis et al., 2013). In these models which focused principally on components of carbon
414 and nutrient cycling, ecosystem properties were linked to plant height and easily
415 measureable leaf traits such as dry matter content and nitrogen concentration, with additional
416 effects of soil parameters. Both traits and soil parameters were related to grassland
417 management to produce ES maps (Figure 5). These models were also applied to project
418 effects of combined climate and socio-economic scenarios translated into grassland
419 management projections and parameterised from observations and experiments (Lamarque
420 et al., 2014).

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

431 Increasing trait data availability through communal data bases and remote sensing offers
432 high promises for the development of trait-based models of ES (Table 2a). There are definite
433 geographic gaps, but overall European vegetation tends to be increasingly well covered,
434 although more extreme environments such as Mediterranean or alpine, where intraspecific

435 variability hinders the use of data measured in more temperate regions, still require collection
436 efforts.

437

438 **Strengths and weaknesses for practice**

439 Although trait-based models of ES supply are in their infancy they rely on rapidly increasing
440 conceptual and empirical evidence. Such models also provide a mechanistic basis for the
441 understanding of biophysical bundles and trade-offs in ES supply (Lavorel and Grigulis,
442 2012; Mouillot et al., 2011). The existence of so called ‘response – effects overlaps’ (Lavorel
443 and Garnier, 2002; Suding et al., 2008) enables mechanistic ES projections under future
444 scenarios using relatively simple models (Lamarque et al., 2014). As with any statistical
445 model however, the greatest care should be taken when attempting to apply such models
446 beyond the parameter space for which they were derived. So far trait-based ES models have
447 rarely been validated across sites, although inter-site analyses have identified generic trait-
448 based models of fodder production, fodder digestibility and litter decomposability (Fortunel et
449 al., 2009; Gardarin et al., 2014; Lavorel et al., 2013b), and the model by Gardarin et al.
450 (2014) was applied to map fodder quality at national scale (Violle et al., 2015). Lastly, trait-
451 based models will become increasingly attractive as trait data bases become more generally
452 available, although the lack of soil data layers in many regions will remain problematic.

453

454 **3.5. Full process-based models**

455 Full process-based models of (terrestrial) ecosystems rely on the explicit representation,
456 using mathematical formulations, of ecological, physical, and biogeochemical processes that
457 determine the functioning of ecosystems. The predictive algorithms simulate a large range of
458 variables, which can then be post-processed to quantify ES. Process-based models have
459 been most widely applied to quantify i) climate regulation (Bayer et al., 2015; Duarte et al.,
460 2013; Metzger et al., 2008; Naidoo et al., 2008; Ooba et al., 2012; Watanabe and Ortega,
461 2014), ii) water supply, water quality, flood and erosion regulation (Gedney et al., 2006;
462 Lautenbach et al., 2012a; Lautenbach et al., 2013; Logsdon and Chaubey, 2013), iii) food,
463 fodder, and bioenergy provision (Bateman et al., 2013; Beringer et al., 2011; Lindeskog et
464 al., 2013; Müller et al., 2014), iii) natural hazard regulation (Elkin et al., 2013), but also in the
465 wider frame of habitat characterisation (Hickler et al., 2012; Huntingford et al., 2011). Here,
466 we discriminate between large-scale and local to landscape scale process-based models.

467 [Appendix 1 lists examples using Dynamic Vegetation Models \(DVM\) \(LPJ-GUESS and](#)
468 [LPJmL: Bondeau et al., 2007; Sibyll et al., 2013; Sitch et al., 2003; Smith et al., 2001\), Earth](#)
469 [System Models \(ESM\) \(JULES and ORCHIDEE: Cox, 2001, Krinner et al., 2005; Zaehle and](#)
470 [Friend, 2010\), hydrological models \(SWAT and others: Neitsch et al., 2005; Stürck et al.,](#)
471 [2014\), forest dynamic models \(e.g. Elkin et al., 2013; Bugmann, 1996\) and models for](#)
472 [ecological restoration \(e.g. Chen and Twilley, 1998; Duarte et al., 2013\). Figure 6 represents](#)
473 [the typical steps of ES assessments with process-based models and possible mapping](#)
474 [outputs.](#)

475

476 Large-scale process models

477 Several large-scale process models have been used for ES quantification. Dynamic
478 Vegetation Models (DVMs) and Earth System Models (ESMs) are large-scale models that
479 provide functional representations of plant and ecosystem processes that are universal
480 rather than specific to one biome or region (Prentice and Cowling, 2013). Hydrological
481 models represent water-related processes within river catchments (Gudmundsson et al.,
482 2012). Global models typically apply a spatial resolution of $0.5^\circ \times 0.5^\circ$, but can be run at finer
483 resolution, or even ecosystem scale if the required drivers are available. In that case, model
484 adjustment might be necessary (e.g. re-calibration, re-formulation to better account for
485 important processes of the region). Applications of these models that include a
486 representation of regional specific features are often designed for local to regional scale
487 application, like forest dynamic models and crop models.

488 This type of models uses a set of process formulations for representing key biogeochemical
489 and physical processes as a function of prevailing atmospheric CO_2 concentration, climate,
490 soil characteristics and eventually land use and management or nutrient deposition.
491 Vegetation is represented as a mixture of plant functional types (PFTs) or species that are
492 distinct in terms of bioclimatic limits and ecological parameters (see Lavorel et al., 2007;
493 Woodward and Cramer, 1996), simulated or prescribed. Age or size classes may be
494 distinguished, but more typically the modelled properties represent averages of the entire
495 grid cell population of a given PFT (Prentice et al., 2007), possibly under a given
496 management type. Soil profile is described using up to ten layers. Hydrological models
497 consider also shallow and deep aquifer storages, and a river routing module simulates the
498 discharge to the rivers network. "Fast" processes are modelled on a daily or sub-daily basis
499 and include energy and gas exchange, photosynthesis, respiration and plant-soil water
500 exchanges. Processes with seasonal dynamics such as plant phenology, growth and
501 biomass allocation are implemented on a daily or monthly basis. Mortality, disturbance,
502 management, are represented on an annual or sub-annual basis, eventually stochastically.
503 By using a small number of PFTs which represent a low-dimensional continuum of plant trait
504 combinations, process-based models generally underestimate the functional diversity of biota
505 in favour of a manageable number of classes. Yet the rise of super computers allows to run
506 DVMs with flexible individual traits (Sakschewski et al., 2015), making it possible to account
507 for functional diversity.

508

509

510 Local to landscape scale process models

511 At local to landscape scales, forest dynamic models with similar philosophy and structure as
512 DVMs have been used for the assessment of bundles of ecosystem services including timber
513 production, natural hazard regulation (avalanches, rockfalls), carbon sequestration,
514 conservation of forest diversity for greater drought resilience and habitat for protected bird
515 species (Elkin et al., 2013; Grêt-Regamey et al., 2008; Temperli et al., 2012).

516 As another type of full-process models with strong potential for ES modelling, watershed
517 models have been designed to simulate hydrological flows and often water quality at the

518 landscape to regional scale. Soil infiltration, surface and subsurface flows as well as
519 evapotranspiration and snowmelt are the main hydrological processes. For modelling water
520 quality the transport and turnover of nutrients and other chemicals need to be represented as
521 well as soil erosion processes, along with agricultural practices. Given the importance of
522 vegetation for the water cycle a vegetation growth model is part of all watershed models.
523 Specifically differences between different plants (or plant functional types) are considered for
524 water use, and in nutrient use for crops. As an example, Stürck et al. (2014) quantified the
525 supply of flood control by running a hydrological model for a number of representative
526 catchment types to quantify the regulating effect of different land use types in different
527 positions in the catchments. Results were extrapolated on a European map accounting for
528 catchment type, location in the catchment, land use and soil conditions. The soil water
529 assessment tool (SWAT) (Neitsch et al., 2005) is an example of an advanced watershed
530 model applied to agricultural landscapes map water purification services (Lautenbach et al.,
531 2012a), to assess fresh water provisioning, fuel provisioning, erosion regulation and flood
532 regulation (Logsdon and Chaubey, 2013) and to describe trade-offs between food and fodder
533 provisioning, biofuel provisioning, water quality regulation and discharge regulation
534 (Lautenbach et al., 2013) depending on crop rotations and crop management.

535

536 For marine ecosystems, the Ecopath with Ecosim (EwE) modelling approach supports
537 predictions of changes in fish to evaluate ecosystem effects of fishing, explore management
538 policy options, analyse impacts and placement of marine protected areas, predict movement
539 and accumulation of contaminants and tracers and model the effects of environmental
540 changes. At the core of EwE is Ecopath, a static, mass-balance snapshot of fisheries based
541 on a set of linear equations combining net production that reflects the balance of catch,
542 predation and other sources of mortality, migration, biomass accumulation, with respiration
543 and unassimilated food. , The Ecosim and Ecospace modules then build on this basic mass-
544 balance module to simulate respectively temporal dynamics using differential equations, and
545 spatial dynamics using spatially explicit distribution of habitat types and fishing effort, along
546 with lateral movement. Alcamo et al. (2005) applied EwE to model fish consumption and
547 production for three important regional marine fisheries (North Benguela, Central North
548 Pacific and Gulf of Thailand) under the four Millennium Ecosystem Assessment global
549 scenarios, showing that for all scenarios fish catch (by weight) was maintained in North
550 Benguela, not maintained in the Central North Pacific, whereas results were scenario-
551 sensitive in the Gulf of Thailand. Another process-based model is available for the long-term
552 carbon sequestration expected from seagrass restoration programmes (Duarte et al., 2013)
553 by combining models of patch growth, patch survival in seagrass planting projects and
554 estimates of seagrass CO₂ sequestration per unit area for the five seagrass species
555 commonly used in restoration programmes. Results enable the estimation of an optimal
556 planting density to maximise C sequestration.

557

558 **Strengths and weaknesses for practice**

559 There is a substantially overlapping set of physiological and ecological principles that is used
560 across process-based models to represent ecosystem dynamics and matter flows, providing

561 robustness and scalability to these models for ES quantification. However, predictions of
562 response variables, e.g. net primary productivity, vary considerably among individual large-
563 scale models (e.g. Denman et al., 2007; Friedlingstein et al., 2006; Sitch et al., 2013). This is
564 due to the lack of a universal set of benchmarks e.g. for terrestrial carbon cycle modelling,
565 and the lack of consensus about several aspects of ecological processes (Prentice and
566 Cowling, 2013). Conversely, local and landscape scale process models can be limited by
567 detailed parameterization and calibration needs and by availability of case-specific validation
568 data.

569 Most process models have not been designed to model ecosystem services but to model the
570 underlying ecosystem functions from which an ecosystem service is derived directly or
571 indirectly. The great strength of this approach is that it allows scenario analysis and if-then-
572 else experiments if the model has been proven to capture the essential system behaviour.
573 Because they model processes and their fundamental biological and physical interactions
574 they also appear particularly promising for exploring mechanisms underpinning synergies
575 and trade-offs between ES (Viglizzo et al., 2016).

576

577

578 **4. Discussion**

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

593

594 **4.1. Future avenues for increasing biophysical** 595 **realism in ES mapping**

596 Plant and Ryan (2013) identified the lack of an 'ES toolbox' as a barrier to the adoption of ES
597 by natural resource managers. While this paper does not attempt to produce such a tool box,
598 it provides a basis for guiding model choice by scientists and practitioners. Here, we
599 identified two important dimensions which enable the incorporation of greater biophysical
600 realism in models supporting ES mapping and can be developed into different model

601 categories regardless of their baseline complexity. First, while simple land cover information
602 is most commonly used to map ES, effects of land use configuration and land use intensity
603 that can be captured by phenomenological models are too often ignored (Verhagen et al.,
604 2016). Recent practice also shows the benefits of incorporating explicit land use rather than
605 simple land cover information for the simplest proxy-based models all the way to advanced
606 full process-based models. Second, approaches incorporating explicitly the role of ES
607 providing biota are emerging as powerful methods to reduce uncertainty in ES mapping. This
608 includes models quantifying individual species effects, species diversity, functional traits, and
609 ecosystem functions described in this review, and for which tools and data are becoming
610 increasingly available. Our review also helps the selection of appropriate methods according
611 to spatial scale, given that scale effects have so far been poorly considered in ES research
612 (Grêt-Regamey et al., 2014b). Review of practice highlights (1) the predominant effect of
613 scale on model selection for practical case studies, (2) the prospect within a single case
614 study to combine different model types, of varying complexity and detail in the representation
615 of biotic effects, depending on specific ES of interest, skills and data / resources availability.

616 The last point highlights that our categories of methods are not necessarily exclusive and
617 there may be more of a continuum between approaches. Hybridization is a fruitful avenue for
618 model improvement depending on context, scale, skills and data availability. This is
619 illustrated by a number of published examples and ongoing developments that gradually help
620 progressing from MAES Tier 2 to Tier 3, by gradually incorporating more mechanistic
621 approaches (Grêt-Regamey et al., 2015), and especially a greater integration of explicit
622 biodiversity effects into mapping of ES supply. For instance, Grêt-Regamey et al. (2008)
623 demonstrated how statistical, phenomenological and process-based models of varying level
624 of complexity can be coupled with a GIS platform in order to assess ecosystem services at
625 landscape scale. Stürck et al. (2014) used a hybridization between a process-based
626 hydrological model and a spatial proxy, look-up approach to map flood regulation across
627 Europe by determining the regulating capacity of different land use-soil combinations within a
628 catchment. Schirpke et al. (2013) coupled the USLE phenomenological model of soil erosion
629 with a semi-mechanistic statistical model of plant root trait effects on soil retention to quantify
630 effects of land use change on soil stability. Large scale full-process models are also evolving
631 towards the integration of trait-based approaches rather than using a small number of fixed
632 Plant Functional Types. First, global vegetation models can be reformulated to incorporate
633 plant traits and their trade-offs as drivers of vegetation distribution (Reu et al., 2011).
634 Second, recent models have started considering direct trait-based formulation (Scheiter and
635 Higgins, 2009; Zaehle and Friend, 2010) and/or parameterisation (Verheijen et al., 2013;
636 Wullschleger et al., 2014). Lastly, for landscape to regional scales so-called 'hybrid' DVMs
637 pave the way to the integration of niche-based models with dispersal models (Midgley et al.,
638 2010) and with trait-based process models (Boulangeat et al., 2012), thereby opening new
639 perspectives for the refinement of the trait-based modelling of ES supply under scenarios of
640 climate change (Boulangeat et al., 2014). Together, all these recent developments illustrate
641 how increasing fundamental understanding on the role of different facets of biodiversity for
642 ecosystem functioning and ecosystem services (Cardinale et al., 2012) can be incorporated
643 into the spatially explicit modelling of ecosystem service supply.

644

645 Quantifying and mapping marine ecosystem services has lagged behind efforts for terrestrial
646 ecosystems, but this is in the process of changing (Liquete et al., 2013; Maes et al., 2012).
647 Data and methods to assess the provision of services from the marine environment are far
648 behind to those available for terrestrial environments (Barbier, 2012; Costanza, 1999). The
649 gap is greatest when it comes to the mapping of ES, the main reasons behind this is the lack
650 of high-resolution spatial information for habitat and species distribution and the incomplete
651 understanding of ecosystem processes and functions within a highly dynamic three-
652 dimensional environment with fluid boundaries (Maes et al., 2012). However, efforts towards
653 mapping marine habitats are increasing. In order to rapidly move towards biophysically
654 realistic mapping, some large fundamental knowledge gaps regarding ecosystem processes
655 need to be resolved. First, there is a lack of information at which scales ecosystem
656 processes and functions occur and how these relate to the provisioning of services. Second,
657 the relationships between biodiversity and ecosystem functions in marine ecosystems are
658 still poorly known (Bergström et al., 2015; Moore et al., 2015). The literature search on
659 marine models/mapping conducted as part of this review highlighted a considerable number
660 of studies which stopped at the assessment or prediction of ESP distributions without taking
661 the next step in analysing their implications for ES provision (e.g. Albouy et al., 2013;
662 Bergström et al., 2015; Moore et al., 2015). Although this is not an easy problem, experience
663 from terrestrial ecosystems in the integration of biotic processes and biodiversity effects into
664 ES quantification and mapping may speed up progress for marine and coastal ecosystems.

665

666 **4.2. Uncertainty and validation of spatially-explicit** 667 **models of ES supply**

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

673 Uncertainty can be conceptually separated into uncertainty about the model structure,
674 uncertainty of model parameterization, uncertainty in the data and last but not least the
675 conceptual uncertainty of the definition of an ecosystem service and underlying processes. In
676 reality all these different components interact: data availability – especially at larger scales –
677 drives in many situations the choice of proxys and the model structure for assessing an ES
678 (Andrew et al., 2015). The use and parameterization of a model is limited by the availability
679 of data – this can in turn lead to suboptimal decision about model structure which leads in
680 turn to an increase in uncertainty. Choosing strongly simplified proxy-models to best match
681 data availability may lead to ignoring the most important processes determining ecosystem
682 service supply, and especially biotic processes. For ecosystem services that predominantly
683 rely on mobile biota – such as pest control, or pollination - increased system understanding
684 on how the different components of biodiversity affect ES provisioning of the services
685 supports the development of more robust models suitable for spatial and temporal
686 extrapolation (Kremen et al., 2007). At the same time, using the most advanced process

687 models in the absence of data to parameterise them at the desired scale does not
688 necessarily lead to higher accuracy. Still, incorporating at least phenomenological
689 understanding into ES models would likely increase reliability and robustness of ES
690 assessments and maps. The use of remote sensing data to estimate ecosystem service
691 proxies (Ayanu et al., 2012; de Araujo Barbosa et al., 2015) and to derive information on
692 biodiversity (O'Connor et al., 2015; Schmidlein et al., 2012) (Table 2) is promising to
693 overcome some of the data limitations, although the derivation of information from remote
694 sensing data requires the use of additional models that bring in their own sources of
695 uncertainty (Foody and Atkinson, 2002).

696

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

708

709 As the availability on species, phylogenetic and functional biodiversity increases currently,
710 along with remote sensing derived information, data availability is likely to become less
711 limiting for using more advanced models (Table 2). But then uncertainty in biodiversity input
712 data could propagate in ES models (Dong et al., 2015). Researchers will then need to
713 estimate the effects of increasing model complexity both on feasibility of parameterisation
714 and on sensitivity to uncertainty in the input data, and to carefully assess potential
715 mismatches in temporal and spatial scale of the new data (Orth et al., 2015; Perrin et al.,
716 2001). First, a specific source of uncertainty in ES assessment relates to the scale of the
717 input data. Although the selection of the modelling scale should be driven by the
718 requirements of the end user (the scale of the decision to be made) (Grêt-Regamey et al.,
719 2014b), data availability seriously limits the degrees of freedom for the selection of input
720 data. There should always be a match between the resolution for ESP biota and
721 environmental data. This in particular applies to climate, where downscaled layers need to be
722 available or calculated for adequate species distribution or process modelling. Conversely,
723 care should also be taken in combining high resolution soil maps with biota data with a
724 coarser resolution (Grêt-Regamey et al., 2014b). Second extrapolating models beyond the
725 range of calibration data is a critical source of uncertainty. Black box statistical models, e.g.
726 some phenomenological, [niche-based](#) or trait-based models that have been (over-)fitted to
727 data without ensuring a robust model structure are especially prone to effects of
728 extrapolation. In general, for an analysis of temporal changes or for assessing management
729 options the projected effects should be compared to the sensitivity of the model outputs

730 against reasonable parameter changes: if the direction of the effect changes or if the
731 magnitude of the response is weaker than the sensitivity of the model one should hesitate to
732 draw strong conclusions from the model. Examples for this approach can be found in
733 (Lautenbach et al. (2011) and (Schulp et al. (2014b)). It is also possible to test the sensitivity
734 towards the uncertainty in the input data, an approach followed in Lautenbach et al. (2012b).

735

736 Thus, ES map users should be aware of the different sources of uncertainty and map
737 creators should at least list them with respect to their application. In addition to this
738 qualitative step a quantitative assessment of the uncertainties of model output should be
739 given. If observed data is used for model parameterisation and calibration, it should be
740 always possible to quantify the uncertainty attached. If no observed data is available against
741 which model output could be compared sensitivity analysis is an option to quantify
742 uncertainties. Lastly, validation of ES models is complicated by the fact that many ES cannot
743 be directly measured. Water purification for example has to rely on water quality data not on
744 measured purification rates (Lautenbach et al., 2012a). Therefore, model validation is often
745 pattern-oriented, considering proxy-data, and tries to at least capture the system behaviour
746 instead of specific process variables.

747

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

751

752

753 **5. Conclusion**

754 In order to achieve the ambitious political agenda for biodiversity, and to support sustainable
755 development that both preserves and benefits from natural capital and ecosystem services,
756 considerable progress is still needed in the practice of quantifying ecosystem service supply.
757 Today a rich array of methods are available, especially for terrestrial systems, that enable the
758 incorporation of biodiversity effects on ecosystem functioning into quantitative, spatially-
759 explicit assessments of ecosystem service supply. We have summarised the main
760 characteristics, strengths and weaknesses of different approaches for mapping ES supply,
761 highlighting their complementarity depending on scale, assessment objectives and context,
762 available skills and data. Review of practice illustrates the predominant effect of scale on
763 model selection, and the ability within a single case study to combine different model types,
764 of varying complexity and detail in the representation of biodiversity effects, depending on
765 specific ES of interest, skills and data / resources availability. Besides, model categories are
766 not necessarily exclusive and there may be more of a continuum between approaches.
767 Recent model developments, with innovative hybridization across model types illustrate how
768 increasing fundamental understanding on the role of different facets of biodiversity for
769 ecosystem functioning and ecosystem services can be incorporated into the spatially explicit
770 modelling of ecosystem service supply. As the availability of biodiversity data (species,
771 phylogenetic and functional) increases and the potential for remote sensing of taxonomic and

772 functional diversity becomes realised, the application of more 'biodiversity realistic' models
773 should be able to move to from research to practice. Considerable challenges remain for
774 assessments to embrace good practice in model uncertainty quantification and validation, an
775 upstream research need to still be addressed. Lastly, while the mapping of terrestrial
776 ecosystem service supply is now reaching greater maturity, for marine ecosystems research
777 is still in its infancy. Urgent research needs regard a better understanding of marine
778 biodiversity effects on ecosystem functioning, and at which scales this influences ecosystem
779 service supply. The availability of high resolution data also proves to be an obstacle that
780 needs to be cleared before sound practice can be achieved.

781

782

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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
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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	Primary data sources for Europe	Remote sensing data
Proxy	<p>Land cover maps</p> <p>Vegetation data bases (Chytrý et al., 2011). European Vegetation Archive (EVA)</p> <p>Global Index of Vegetation-Plot Databases (http://www.givd.info) (Dengler et al., 2011)</p> <p>Potential lack of data layers (e.g. soils)</p>	<p>Mapping thematic variables like Land Use/Land Cover, Vegetation, Forest, Wetland, Water, Burnt area, etc.</p> <p>Regional scale (for mapping landscape units), medium spatial resolution data like multitemporal MODIS, Spot Vegetation or MeteoSat data to follow vegetation dynamic.</p> <p>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).</p> <p>(Ayanu et al., 2012 ; Burkhard et al., 2012; Kuenzer et al., 2014 ; Pettorelli et al., 2014)</p>
Phenomenological	<p>Maps or proxy of landscape elements (van der Zanden et al., 2013)</p> <p>Topographic information including Digital Elevation Models: road networks, river networks (Lehner et al., 2004), coastlines (USGS HYDRO1K, 2015)</p> <p>Biophysical data including soil data (European Soil database see Panagos et al., 2012)</p>	<p>As for proxy models</p>
Niche-based	<p>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).</p> <p>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).</p> <p>Extensive distribution data available for 1280 higher plants; digitized Atlas Flora Europea. Trees: exhaustive data at 1 km² resolution (http://www.efi.int/portal/virtual_library/information_services/mapping_services/tree_species_maps_for_european_forests/).</p> <p>More comprehensive species distribution data available on a country per country basis, and for specific regions within a same country.</p> <p>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</p>	<p>Texture variables like object size and shape, compactness, homogeneity/heterogeneity, neighborhood relationships, fragmentation, connectivity, relevant for plant type specification and habitats characterization.</p> <p>Global scale, Meteosat or SpotVegetation.</p> <p>Regional scale, medium spatial resolution data like multitemporal MODIS; can characterize vegetation dynamics.</p> <p>(Ayanu et al., 2012 ; Burkhard et al., 2012; Kuenzer et al., 2014 ; Pettorelli et al., 2014)</p>

et al., 2014).

Trait data for functional diversity: see trait-based models

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)), 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 CO₂ 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

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).

	interactions	
	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).	
Full process – local-landscape-scale	<p>Input data (historical and scenarios) as for large-scale process-based models with the additional possibility for local-landscape scale data</p> <p>Climate forcing from observations (e.g. UKCP09)</p> <p>Land-use / land management data: Fuchs et al. 2013, CORINE land cover (EEA, 2012), Salmon-Monviola et al., 2012</p> <p>Detailed DEM and soil quality maps (Krysanova et al., 2005)</p>	<p>The same distinction as above between remote-sensing data for model input data or for model calibration/validation can be made.</p> <p>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, ...).</p> <p>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)</p>

Table 2 – 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	<ul style="list-style-type: none"> - 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) 	<ul style="list-style-type: none"> 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	<ul style="list-style-type: none"> - Sediment and bathymetry charts, point source contaminant data, tidal model outputs, seabed shear stress and expert information (Townsend et al., 2014) 	
Niche-based	<ul style="list-style-type: none"> - 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	<ul style="list-style-type: none"> - Seagrass patch growth, patch survival in seagrass planting projects, estimates of seagrass CO₂ sequestration per unit area (Duarte et al., 2013) 	
Full process – large-scale	<ul style="list-style-type: none"> - Submarine habitat cover (Yee et al., 2014) 	
Full process – local-landscape-scale	<ul style="list-style-type: none"> - Use of biogeochemical model; Dissolved Organic Carbon; Particulated Organic Carbon; nutrients; carbonates; zooplankton; microzooplankton; phytoplankton (Canu et al., 2015) 	

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

Figures

Figure 1 - Biodiversity components incorporated into different categories of models of ecosystem service supply

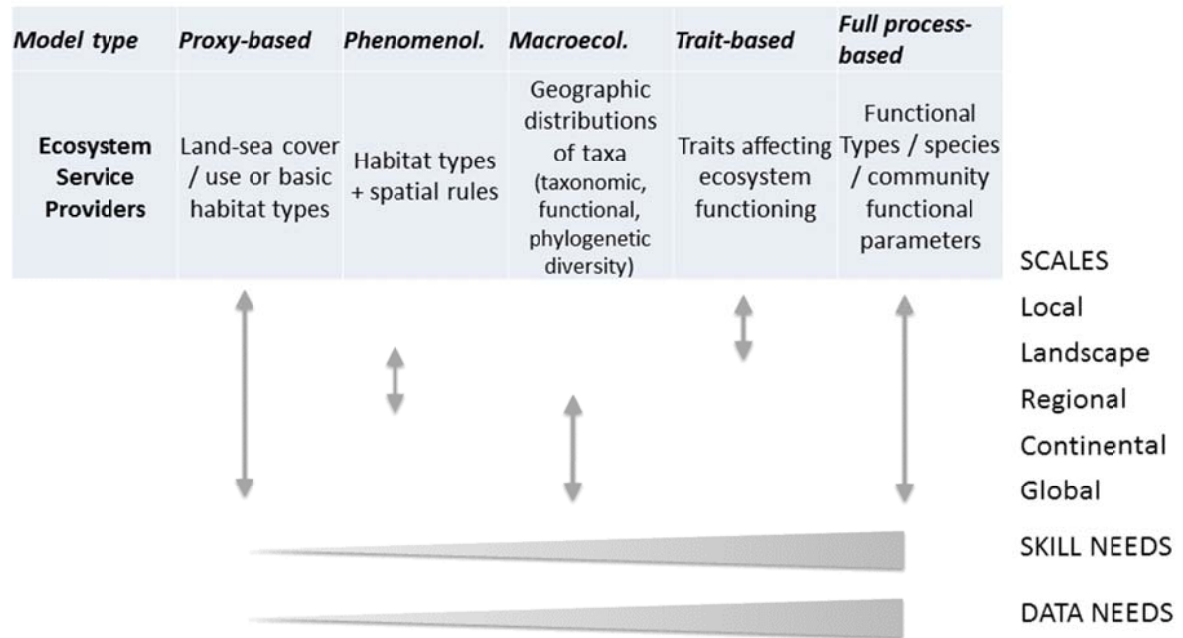


Figure 2 – Proxy-based spatial modelling of five-year average crop production (energy equivalent MG/ha) (2008-2012) for the Grenoble urban area (France). Schematic method identifying crop succession over 5 years at parcel scale using MODIS data for determining winter / spring crops based on phenology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

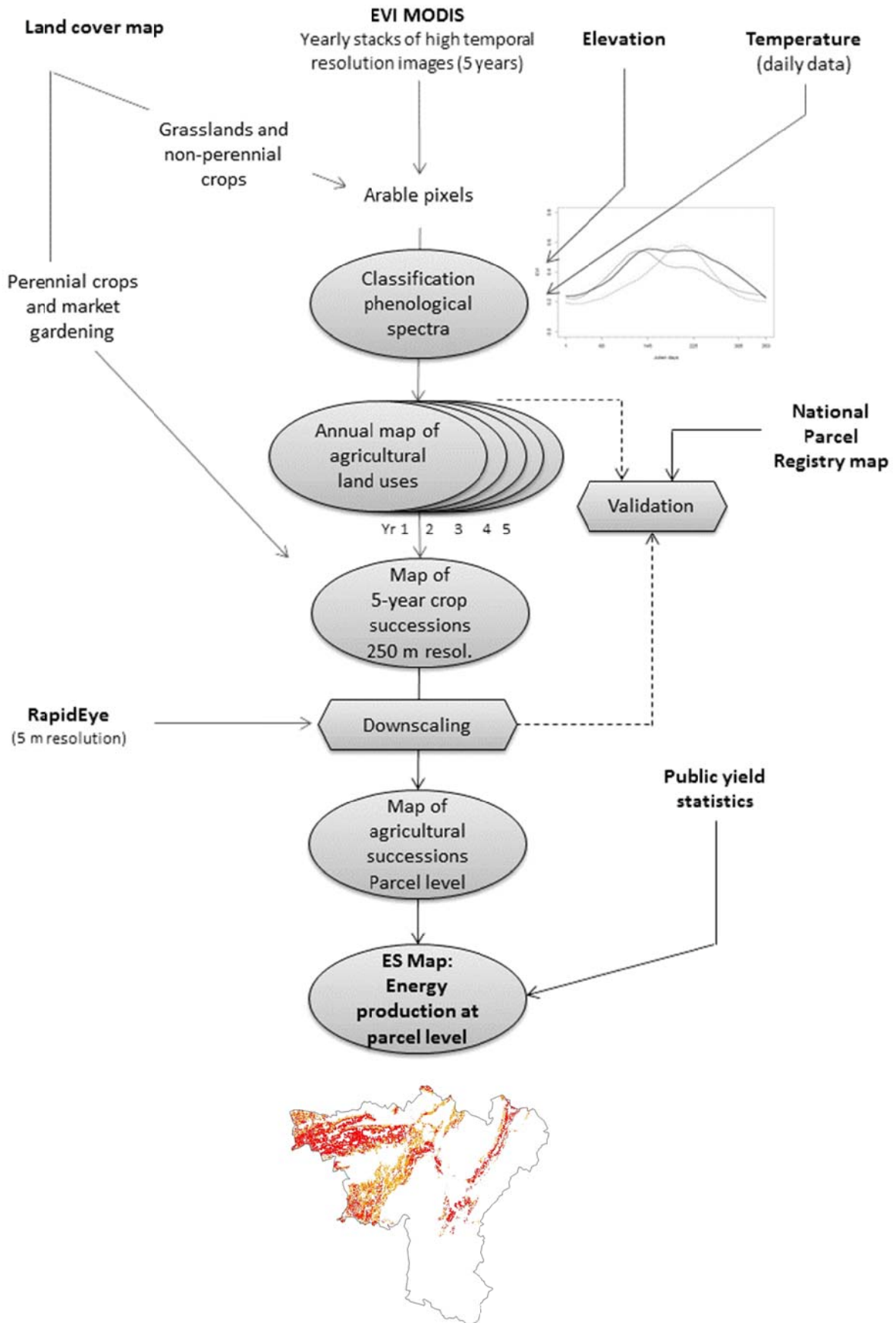


Figure 3 - Phenomenological model development for mapping marine ecosystem services based marine ecological principles. Adapted from Townsend et al., 2014.

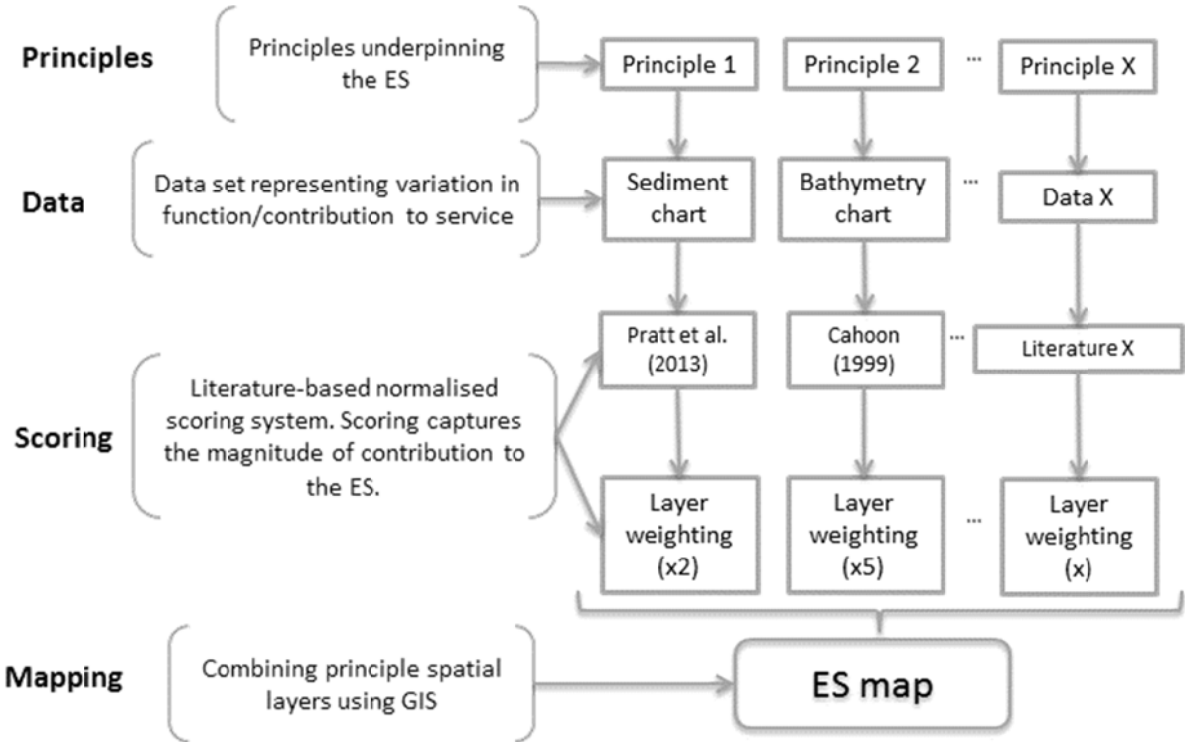


Figure 4 – Macro-ecological models of ecosystem service supply potential. ESP: ecosystem service provider; SDM: species distribution modelling. Here the final map uses richness of vertebrate predators of rodents as an indicator for potential capacity to control rodents in Europe (from Civantos et al.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

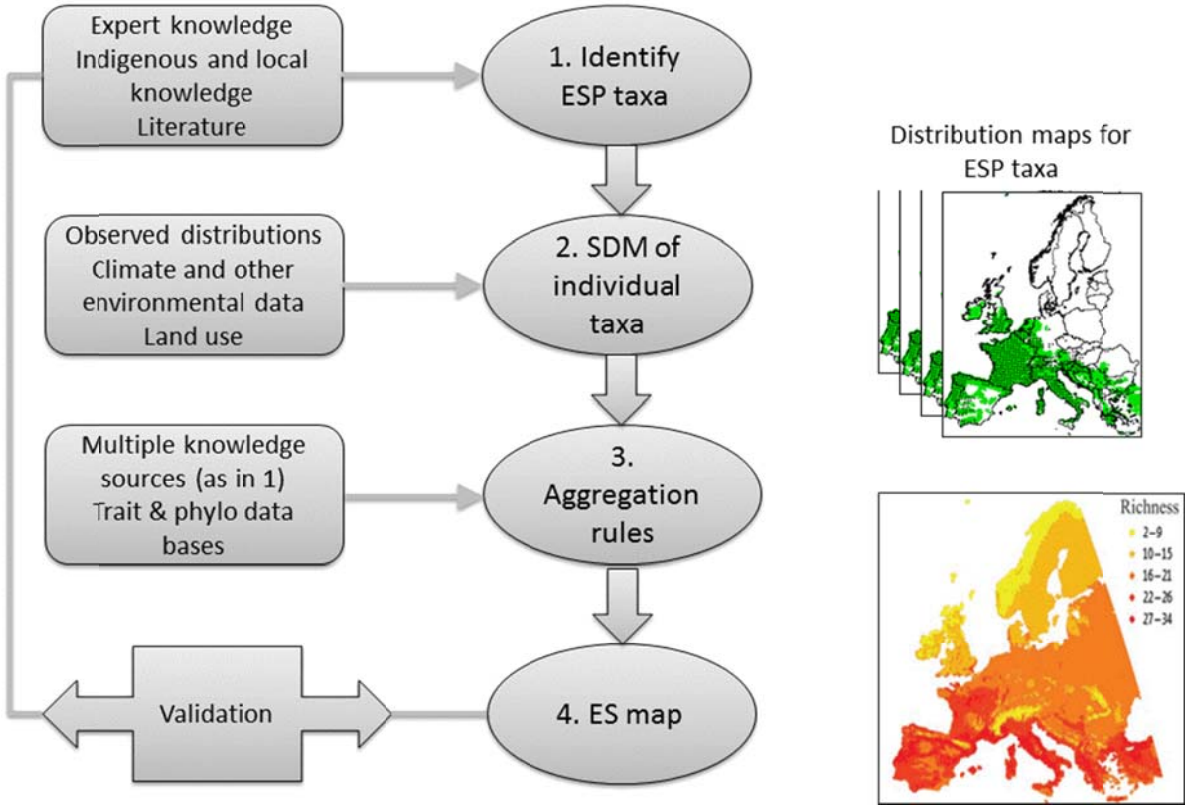


Figure 5 – Trait-based modelling of ecosystem service supply potential for mountain grasslands. Schematic summary of modelling steps based on cascading effects from land use and environmental variables, to community mean plant traits and to ES, illustrated here in the case of fodder production by mountain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

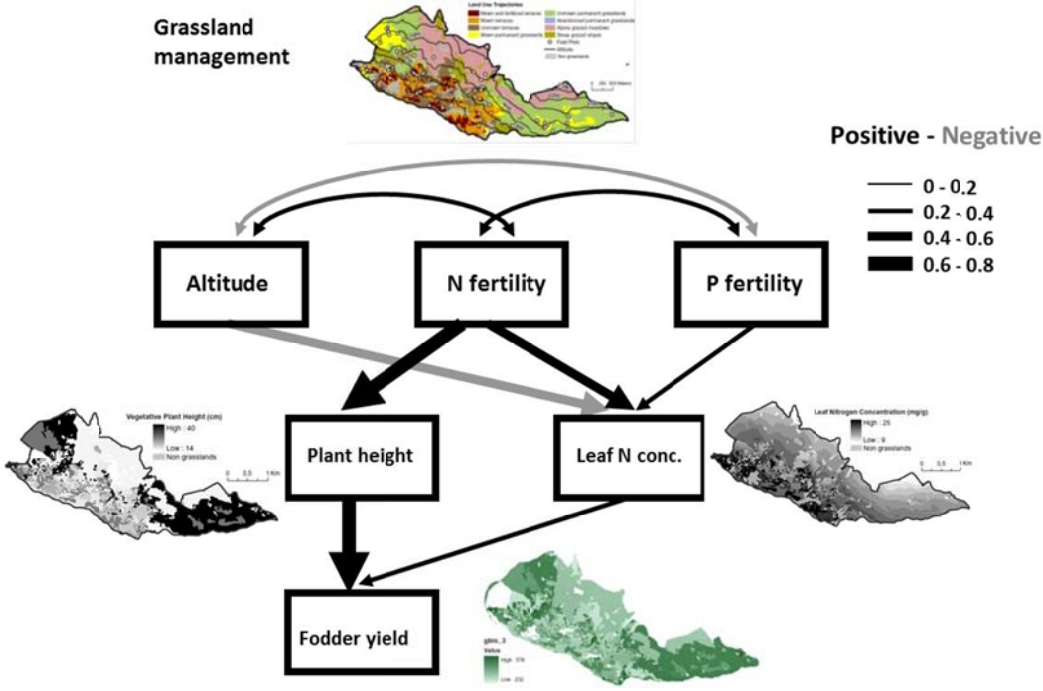
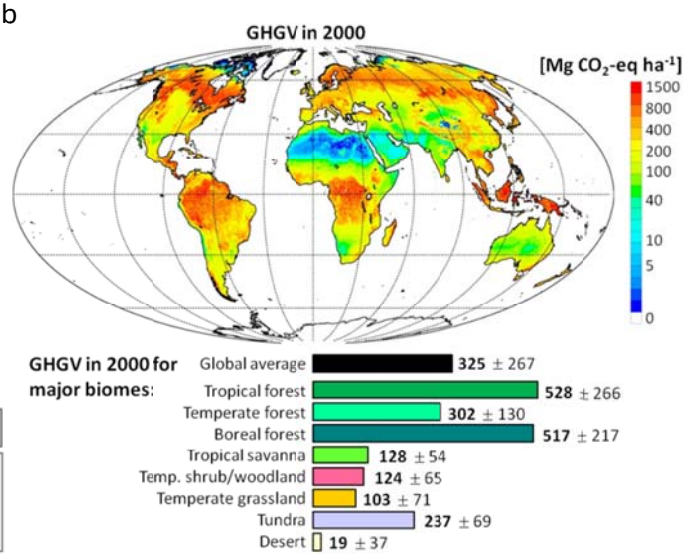
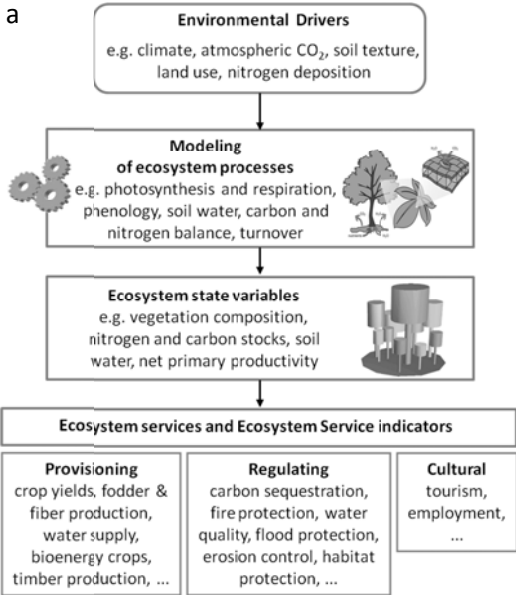


Figure 6 – Workflow typical for process-based models (a). Selected provisioning and regulating services are most often directly linked to simulated ecosystem state variables while cultural services may only be derived from suitable indicators. Example application of a process-based model for the quantification of an ES metric accounting for the full biogeochemical implications of carbon sequestration by estimating contribution of CO₂ to the Greenhouse Gas Value (GHGV) (b) (Figure after Bayer et al., 2015).



Appendix 1

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

Model name	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)	Global climate regulation	Phenomenological	continental (EU)	CLUE
IVM-pollination (Schulp et al., 2014)	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 and Verburg, 2011)	Physical use of land-/seascapes	Phenomenological	continental (EU)	CORINE land cover
Biocontrol (Civantos et al., 2012)	Biocontrol	Niche-based	regional - continental (EU)	CORINE land cover 2000 - although any data base is suitable in principle
Trait-based models of grassland ES (Grigulis et al., 2013; Lavorel et al., 2011)	Grassland forage quantity, forage quality, soil organic matter, leached nitrates, soil fertility, soil stability	Trait-based	landscape	grassland management types

LPJ-GUESS (Sitch et al., 2003; Smith et al., 2001).	Global climate regulation, surface water supply (non-drinking), cultivated crops, fodder; tested: timber, energy crops, soil formation, etc.	Process-based	regional/global	Historical and land-use fractions according to (Hurt et al., 2011), crop species according to MIRCA2000 (Portmann et al., 2010). Usage of CLUMondo tested
LPJmL (Bondeau et al., 2007)	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 et al., 2007). 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 fed by LPJmL (Lotze-Campen et al., 2008; Lotze-Campen et al., 2010)
IVM-FloodRegulation (Stürck et al., 2014)	Flood protection	Process-based	continental (EU)	CORINE land cover 2000

SWAT (Lautenbach et al., 2012)	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., 2015)	Soil moisture, deep water seepage	Process-based	landscape	grassland management types

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

Model name	Abiotic variables			
	<i>climate</i>	<i>soil</i>	<i>landscape pattern</i>	<i>others</i>
IVM-carbon (Schulp et al, 2008)		emission factors: Map with emission factor for each land use type as 1x1 km grids (see calculation rules) (Janssens et al., 2004) & 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)				
IVM-tourism (Van Berkel & Verburg, 2011)			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)	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)		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).	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)	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

IWM-FloodRegulation (Stürck et al, 2014)	precipitation regime (Haylock et al., 2008)	soil water holding capacity classification (FAO, 2009)	DEM and forest and agricultural management variables
SWAT (Lautenbach et al. 2012)	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 evapotranspiration. 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 achievable resolution	terrain (slope)
HILLFLOW (Leitinger et al. 2015)	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	Biotic variables					
	<i>individual species</i>	<i>species diversity indices</i>	<i>Plant Functional Types</i>	<i>Plant Funct. Traits</i>	<i>functional diversity indices</i>	<i>others</i>
IVM-carbon (Schulp et al, 2008)						forest age
IVM-pollination (Schulp et al, 2014)						pollination dependency index per crop; Habitat suitability for bees
IVM-tourism (Van Berkel & Verburg, 2011)						biophysical characteristics (e.g., presence of sea, beach); presence of N2000 areas, HNV farmland, and UNESCO natural monuments
Biocontrol (Civantos et al. 2012)	vertebrate species known as predators of vertebrate or invertebrate pests					
Trait-based models of grassland ES (Lavorel et al. 2011, Grigulis et al. 2013)		plant Shannon diversity			plant community mean vegetative height, leaf N concentration, leaf dry matter content, rooting architecture	microbial functional diversity parameters calculated from plant traits and soil N and WHC

<p>LPJ-GUESS (Smith et al. 2001, Sitch et al. 2003).</p>	<p>11 PFTs e.g. according to (Ahlström et al., 2012); 11 CFTs (Lindeskog et al., 2013)</p>	
<p>LPJmL (Bondeau et al. 2007)</p>	<p>9 PFTs (Sitch et al., 2003), 12/14 annual CFTs, 2 types of managed grass, 3 types of bioenergy plants. 7 perennial crops (Mediterranean version).</p>	
<p>IVM-FloodRegulation (Stürck et al, 2014)</p>		<p>tree species, as part of the forest management variables at 1km scale (Brus et al., 2012)</p>
<p>SWAT (Lautenbach et al. 2012)</p>		<p>The crop.dat we use contains currently 17 generic land use types with vegetation cover (such as pasture, rangeland, deciduous forest), 81 agricultural crops. But this list has been extended e.g. for applications in the tropics.</p>

HILLFLOW (Leitinger et al. 2015)

community mean
root depth,
evapo-
transpiration,
canopy
interception

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

Model name	Ecosystem service (CICES terminology)	Model type	Brief description of model logics
IVM-carbon (Schulp et al, 2008)	Global climate regulation	Phenomenologica I	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 sequestration 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)	Pollination	Phenomenologica I	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)	Physical use of land- /seascapes	Phenomenologica I	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 are weighted by a factor for symbolic capital.
Biocontrol (Civantos et al. 2012)	Biocontrol	Niche-based	niche-based 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)	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)	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)	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 Ecosystem Services.
IVM-FloodRegulation (Stürck et al, 2014)	Flood protection	Process-based	The STREAM hydrological model is applied to several catchments 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 (Ramankutty and Foley, 1999)) to determine target areas where vegetation could

			enhance flood regulation supply
SWAT (Lautenbach et al. 2012)	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., 2005). 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., 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.
HILLFLOW (Leitinger et al. 2015)	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	Main strengths	Limitations
<p>IVM-carbon (Schulp et al, 2008)</p>	<p>able to detect changes in carbon sequestration following land use change at coarse levels; applicalbe across many EU countries;</p>	<p>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)</p>
<p>IVM-pollination (Schulp et al, 2014)</p>	<p>incorporation of both mapping demand and supply; applicable across many regions; level of detail can be nehanced by parameterizing the model for individual species</p>	<p>difficult to validate results, assumption of habitat uniformity, variation in timing of pollination demand and supply within a year not accounted for</p>

IVM-tourism (Van Berkel & Verburg, 2011)	Applicable across the EU; using easy accessible 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
Biocontrol (Civantos et al. 2012)	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
Trait-based models of grassland ES (Lavorel et al. 2011, Grigulis et al. 2013)	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

LPJ-GUESS (Smith et al. 2001, Sitch et al. 2003)	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)
LPJmL (Bondeau et al. 2007)	Closed carbon cycle, consistent representation of the biogeochemical processes bewteen the different plant types.	Currently no nitrogen cycle
IVM-FloodRegulation (Stürck et al, 2014)	Combination of flood regulation demand and supply to identify priority 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

SWAT (Lautenbach et al., 2012)	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.
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HILLFLOW (Leitinger et al. 2015)	Mechanistic understanding of ES supply depending on vegetation functioning	Not a detailed hydrological model; requires heavy site measurements for parameterisation
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Appendix 1 - Table 2a - Part 1 - Marine Model Variables

Model name	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)	Provisioning, nutrition, biomass (fish production)	Niche-based	regional	NA
Mercury sequestration (Anastacio et al 2013)	Mediation of waste, toxics and other nuisances	Process-based	regional	NA
Spatial model of coastal ecosystem services (Barbier 2012)	mediation of flows (storm protection) & fish density	NA	local	NA
Hydrodynamic model (Temmerman et al 2012)	Mediation of flows (flood protection)	Phenomenological	local	NA
Hydrodynamic model (Shepherd et al 2007)	Maintenance of physical, chemical and biological conditions (nutrient removal and carbon sequestration)	Phenomenological	local	NA
Mangrove's wind protection (Das et al, 2013)	Mediation of flows (wind protection)	Phenomenological	regional	NA
CO₂ capture potential of seagrass restoration (Duarte et al, 2013)	Maintenance of physical, chemical and biological conditions (carbon sequestration)	Trait-based	local	NA

Multiscale ecological and economic models salmon, shrimp & blue crab (Jordan et al 2012)	Provisioning, nutrition, biomass (food production)	Phenomenological	local & regional	NA
Coastal protection (Liquete et al 2013)	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)	multiple ES (provisioning, cultural, supporting)	Spatial proxy-based	local	NA
InVEST Marine carbon storage & sequestration (Guerry et al 2012)	Carbon storage & sequestration	Spatial proxy-based	local / regional / continental	NA
InVEST Food provision (Guerry et al 2012)	Food provision	Spatial proxy-based	local / regional / continental	NA
InVEST Marine renewable energy (Guerry et al 2012)	Energy	Spatial proxy-based	local / regional / continental	NA

InVEST Recreation (Guerry et al 2012)	Recreation	Spatial proxy-based	local / regional / continental
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Appendix 1 - Table 2a - Part 2 - Marine Model Variables

Model name	Abiotic variables			
	<i>climate</i>	<i>soil</i>	<i>landscape pattern</i>	<i>others</i>
Ecosim/EcoPath (Alcamo et al, 2005)	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)				Hg in biomass (several variables, Hg in belowground biomass, Hg exiting biomass, incorporation 365 days ago...), temperature, salinity, cloud cover
Spatial model of coastal ecosystem services (Barbier 2012)				Distance to the ecosystem, distance from seaward edge
Hydrodynamic model (Temmerman et al 2012)	x		x	
Hydrodynamic model (Shepherd et al 2007)		x	x	Elevation; management variables;
Mangrove's wind protection (Das et al, 2013)	x			% damaged houses, impact of the storm, wind velocity, velocity of the storm surge, surge height, distance from the coast
CO2 capture potential of seagrass restoration (Duarte et al, 2013)	x			

<p>Multiscale ecological and economic models salmon, shrimp & blue crab (Jordan et al 2012)</p>	<p>Fishery landings, effort data, habitat GIS coverages, survival rates for habitat types, salinity, economic value salmon fisheries</p>
<p>Coastal protection (Liquete et al 2013)</p>	<p>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</p>
<p>Role of eelgrass in ES, food web modeling (Plummer et al 2013)</p>	<p>No abiotic variables stated</p>
<p>InVEST Marine carbon storage & sequestration (Guerry et al 2012)</p>	<p>Carbon stored, rate of C accumulation in sediments, economic information such as market/non-market value of stored/sequestered Carbon</p>
<p>InVEST Food provision (Guerry et al 2012)</p>	<p>Fishing fleet distribution, value of landings, fishing grounds distribution, price of harvested product, harvest rate information</p>
<p>InVEST Marine renewable energy (Guerry et al 2012)</p>	<p>wave condition data (height, peak period, technological capabilities (e.g. Performance tables, maximum capacity)</p>
<p>InVEST Recreation (Guerry et al 2012)</p>	<p>visitation rates, recreational activities</p>

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

Model name	Biotic variables						Ecosystem type
	<i>individual species</i>	<i>species diversity indices</i>	<i>Plant Functional Types</i>	<i>Plant Functional Traits</i>	<i>Functional diversity indices</i>	<i>others</i>	
Ecosim/EcoPath (Alcamo et al, 2005)	x					Trophic flows, biomass, production, mortality, exports, biomass accumulation, biomass of functional groups, consumption, catch data, trophic behaviours, landings, discards, fishing effort, human population development	marine
Mercury sequestration (Anastacio et al 2013)							tidal wetlands
Spatial model of coastal ecosystem services (Barbier 2012)						Thread of ecological collapse	mangrove habitat
Hydrodynamic model (Temmerman et al 2012)			tidal wetlands				tidal wetlands
Hydrodynamic model (Shepherd et al 2007)							tidal wetlands and mudflats

(estuary)

Mangrove's wind protection (Das et al, 2013)	x	mangrove forest	distance from mangrove forest, mangrove forest extent	mangrove forest
CO₂ capture potential of seagrass restoration (Duarte et al, 2013)	x	seagrass meadows	patch growth, patch survival in seagrass planting projects, estimates of seagrass CO ₂ sequestration per unit area for five seagrass species	seagrass meadows
Multiscale ecological and economic models salmon, shrimp & blue crab (Jordan et al 2012)	x		stock biomass, net recruitment per year, carrying capacity	marine
Coastal protection (Liquete et al 2013)				marine
Role of eelgrass in ES, food web modeling (Plummer et al 2013)			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)	vegetation distribution maps
InVEST Food provision (Guerry et al 2012)	fish distribution, fish survival, recruitment rate
InVEST Marine renewable energy (Guerry et al 2012)	None
InVEST Recreation (Guerry et al 2012)	habitat distribution

Appendix 1 – Table 2b - Part 1 – Marine Model Application

Model name	Model Category	Ecosystem service	Brief description of model logics
		(CICES terminology)	
Coastal protection (Liquete et al., 2013)	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 Marine carbon storage & sequestration (Guerry et al., 2012)	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)	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)	Spatial proxy-based	Food provision	InVEST model estimates the quantity and monetary value of fish harvested by commercial fisheries. Appropriate 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)	Spatial proxy-based	Energy	Models energy production from waves and models off-shore wind energy production. The model assesses potential wave power and

			energy based on wave conditions and technology-specific capabilities.
InVEST Recreation (Guerry et al 2012)	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
Hydrodynamic model (Temmerman et al., 2012)	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)	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 and Crépin, 2013)	Phenomenological	Mediation of flows (wind protection)	Modeling of wind attenuation and protection offered by mangroves in the event of wind-related damage during storms, specially in areas affected by tangential wind
Ecosim/EcoPath (Alcamo et al., 2005)	Niche-based	Provisioning, nutrition, biomass (fish production)	Fish production (landings) is estimated for three regional fisheries (Gulf 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)	Niche-based	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)	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)	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 community may respond to changes in coverage of native eelgrass (<i>Zostera marina</i>), and how these modeled responses can be assessed using an ecosystem services framework, expressing these services with economic currencies in some cases

			and biological proxies in others.
Mercury sequestration (Anastácio et al., 2013)	Process-based	Mediation of waste, toxics and other nuisances	Modelling of growth and mercury (HG) sequestration by <i>Bolboschoenus maritimus</i> 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 <i>B. maritimus</i> 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
Spatial model of coastal ecosystem services (Barbier, 2012)	NA	mediation of flows (storm protection) & fish density	Modelling of ecological production functions that decline across a coastal landscape

Appendix 1 - Table 2b – Part 2 – Marine Model Application

Model name	Main strengths	Limitations
Coastal protection (Liquete et al 2013)	The assessment shown in the paper could help assist the comparison between European regions and to further national or regional scale studies of ecosystem services. In Europe it can have a direct application on the EU Biodiversity Strategy, the EU Floods Directive. On an international scale, this approach could be taken by CBD (Convention on biological diversity) countries.	The continental scale of the model may oversimplify the local coastal processes, since they cannot be taken into account a the continental scale and resolution. Coastal studies generally lack the step of aggregation of data and knowledge transfer from local case studies to regional ones. Due to the lack of large scale datasets or methodologies some important factors could not be included in the model (e.g. local sediment Budget, subsidence, main direction of morphologic features with respect to wave action, coastal development and management, low vs. high coasts, health of the ecosystems, the specific non-linear response of habitats for protection among others). Further information on limitations or aspects that could improve the model are discussed in the paper.
InVEST Marine carbon storage & sequestration (Guerry et al 2012)	Not stated in the paper	Not stated in the paper
InVEST Coastal protection (Guerry et al 2012)	Not stated in the paper	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

		<p>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</p>
InVEST Food provision (Guerry et al 2012)	Production of maps that identify the most important marine and coastal areas across a variety of fishing fleets	It does not model behavior , for that reason it is not well suited to the evaluation of how human uses may change in response to changes in the marine environment.
InVEST Marine renewable energy (Guerry et al 2012)	Not stated in the paper	Not stated in the paper
InVEST Recreation (Guerry et al 2012)	Not stated in the paper	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.
Hydrodynamic model (Temmerman et al 2012)	Not stated in the paper	Not stated in the paper
Hydrodynamic model (Shepherd et al 2007)	Cost benefit analysis (CBA) demonstrates that managed realignment provides positive economic advantages. In a wider sense the case study demonstrates how CBA of managed realignment schemes should be undertaken so that the potential social cost of realignment can be better understood	The model and CBA is based in many assumptions (e.g. sedimentation rate 1.5 or 6mm per year) and uncertainties (e.g. habitat values or nitrogen removal), however the assumptions are conservative, if anything it will have underestimated the value of the service
Mangrove's wind protection (Das et al, 2013)	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 substantially 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
Ecosim/EcoPath (Alcamo 2005)	Global application	Not stated in the paper
Multiscale ecological and economic models salmon, shrimp & blue crab (Jordan et al 2012)	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.	Not stated in the paper

<p>CO₂ capture potential of seagrass restoration (Duarte et al, 2013)</p>	<p>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</p>	<p>The model presented delivers rough, but conservative, estimates of the average CO₂ capture capacity associated with seagrass restoration projects. These estimates are conservative because they focus on the mean, whereas planting of seagrass patches for CO₂ capture can be managed to achieve maximum capture, which could double the estimates 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.</p>
<p>Role of eelgrass in ES, food web modeling (Plummer et al 2013)</p>	<p>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</p>	<p>Not stated in the paper</p>
<p>Mercury sequestration (Anastacio et al 2013)</p>	<p>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</p>	<p>the value calculated does not include sequestration by other plants sharing the habitat with <i>B. maritimus</i>. 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</p>

		studied area
Spatial model of coastal ecosystem services (Barbier 2012)	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.	Not stated in the paper

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