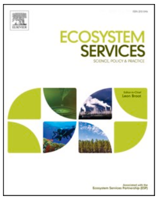
Ecosystem Services 48 (2021) 101259

Contents lists available at ScienceDirect

Ecosystem Services

journal homepage: www.elsevier.com/locate/ecoser



Ecosystem service mapping needs to capture more effectively the biodiversity important for service supply

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ARTICLE INFO

Keywords:
Synergies and trade-offs
Species-based ecosystem services
Europe
Biophysical models of ecosystem services
Multi-scale analysis
Weighted provider richness

ABSTRACT

Large scale mapping of ecosystem services and functions (ES) is an important tool for researchers and policy makers to inform nature management and policies but it relies mainly on ES modelled with biophysical data such as land cover, henceforth biophysical ES. Other ES, henceforth species-based ES, are modelled at small scales based on species providers. As species-based ES are rarely included in multi-service, large-scale spatial assessments, we do not know if these assessments provide accurate information for managing the biodiversity important for species-based ES. We calculate and map weighted provider richness (WPR) for 9 species-based ES by weighting species data in Europe by their functional efficiency derived from functional trait databases. We compare WPR spatial patterns with those of 9 biophysical ES at continental and national scales in Europe. We find positive correlations at continental scale, and weaker positive correlations or neutral relationships at national scale between biophysical ES and WPR. Patterns of synergies and trade-offs for WPR are different from those of biophysical ES and change from continental to national scale. WPR for most species-based ES are synergistic with each other but WPR for existence value has the weakest synergies with other WPRs. Biodiversity data is still insufficient to truly map species-based ES at large scales but WPR can represent the next step forward for spatial ES assessments. A lack of spatial information on species-based ES in large-scale assessments leads to inaccurate information on ES distribution, and their synergies and trade-offs, which can lead to misguided management and conservation decisions.

1. Introduction

Comprehensive and sound spatial assessments are needed to guide conservation and management of ecosystem functions and services (ES) (Maes et al., 2012). To model and quantify ES supply, researchers often use either species-based providers (e.g., functional groups) or biophysical providers (e.g., land cover types) (Luck et al., 2009). Most ES are modelled exclusively based on either biophysical or species-based providers. For example, models of pest control and birdwatching use species-based providers while water regulation and carbon storage are

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https://doi.org/10.1016/j.ecoser.2021.101259
Received 30 March 2020; Received in revised form 29 January 2021; Accepted 4 February 2021

modelled based on biophysical providers (Luck et al., 2009). Species-based providers are used for ES for which the contribution of individual species towards supply can be calculated. Biophysical providers are especially useful for ES for which the contribution of individual species cannot be separated from the contributions of other species or abiotic elements, as is the case, for example, for prevention of soil erosion (Guerra et al., 2014). Because estimating contributions of individual species is usually time consuming and effort intensive, authors sometimes rely on biophysical models even for ES for which contributions of individual species can be calculated in theory (Zulian et al., 2013). This indicates that the underlying ecological processes do not translate perfectly into different methodologies but, for the purposes of this study, we will refer to the two ES categories according to their dominant modeling approach.

Despite both ES categories being important for human wellbeing (MEA, 2005), their influence on conservation planning and policy is unequal. The ES modelled primarily with biophysical data, henceforth biophysical ES, have received more attention due to high-quality remote sensing data and accurate land cover mapping (Maes et al., 2012). Therefore, concepts such as ES hotspots, synergies and trade-offs have been developed based on biophysical ES (Nelson et al., 2009). Species-based service providers and their associated services, henceforth species-based ES, are rarely used in multi-service, large-scale assessments (Civantos et al., 2012; Schulp et al., 2014; Woodcock et al., 2014; Redhead et al., 2018). Consequently, we do not know if the assumptions and spatial patterns of biophysical ES are also useful to conserve and manage species-based ES and the biodiversity supporting them.

Progress in identifying providers of species-based ES and understanding their contributions to species-based ES can bring us a step closer to large-scale, comprehensive ES assessments. Arguably, the best understood service providers are pollinators. The relationship between pollinator richness and pollination at any one particular moment in time is positive but quickly saturating (Kleijn et al., 2015). However, high provider richness is positively correlated with multifunctionality (Isbell et al., 2011) and stability of species-based ES across time and space (Bartomeus et al., 2013; Kleijn et al., 2015; Winfree et al., 2018). Different taxa can contribute additively to one ES, as shown for pest control by Williams-Guillén et al. (2008). The fact that often only a subset of species are responsible for most ES supply (Perfecto et al., 2004) indicates the importance of understanding the functional contributions of service providers, which depends on their functional efficiency and abundance (Kremen, 2005). Although data on species distribution is improving, species abundances remain unavailable at large scales and remains a major obstacle in large-scale mapping of species-based ES. Efficiency of service providers at performing ES can vary across time and space, and can cahnge with community composition. Databases of functional traits (Kattge et al., 2011; Wilman et al., 2014) give a broad understanding of the relative importance of individual species for ES supply.

Here, we calculate a large-scale indicator of species provider richness weighted by functional efficiency for 9 species-based ES in Europe as the best-available proxy of biodiversity contribution to species-based ES. To calculate the weighted provider richness (WPR) indicator we use species distribution data from European biodiversity atlases weighted by measures of their importance for ES. We then compare the WPR spatial patterns to those of biophysical ES (Maes et al., 2012) to understand the similarities and differences relevant for ES conservation and management. Both the species-based ES for which we calculate WPR and the biophysical ES are representative of the broad classes of provisioning, regulating and cultural services according to the definitions of the Millennium Ecosystem Assessment (MEA, 2005). We use here a broad definition of ES that refers to their supply and includes ecosystem functions, a feature representative of large-scale ES assessments (Isbell et al., 2011; Maes et al., 2012). We calculate spatial correlations between increasing (from one to 9) and equal numbers of biophysical ES and WPRs. We analyze synergies and trade-offs between WPR of species-based ES and compare them to synergies and trade-offs between biophysical ES. We conduct all analyses at two spatial extents, henceforth scales, relevant for decision-making in Europe: continental and national. Finally, we discuss the implications of our analysis for current ES conservation and management, and the necessary next steps for more complete ES assessments.

2. Materials and methods

2.1. Weighted provider richness of species-based services

We selected 9 species-based ES: wild food, medicinal plants, fodder, pest control, carcass removal, seed dispersal, existence value, wildlife watching and hunting (Table S1 in Supporting Information). These services are supplied by species, henceforth providers, for which data on spatial distributions are available at continental level in Europe. For most taxa, functional trait databases provide information to estimate functional efficiency for each species-based ES. We calculated WPR for each ES in four steps: 1) identification of providers for each ES, 2) extraction and stacking of the European distributions of providers, 3) weighting of providers by their normalized functional efficiency and calculation of WPR at grid cell level through the weighted sum of providers and 4) normalization of WPR to the interval [0,1].

2.2. Step 1 – Identifying ES providers

For medicinal plants, we used the Plants for a Future database of medicinal ratings (Fern, 1997) containing medicinal ratings from 1 (low medicinal value) to 5 (high medicinal value). We used the medicinal rating as measure of functional efficiency. For wild food, we reviewed the plants' edibility ratings (1–5 range) from the same database (Fern, 1997). We used the plants' edibility rating as measure of functional efficiency. We also included as providers of wild food the mammal and bird species hunted in Europe and representing an important element of national cuisines (Schulp et al., 2014). In the absence of more detailed information, their functional efficiency was assumed for all species equal to the highest functional efficiency in the Future database. In the case of wild fodder, we identified the providers based on the leaf palatability trait (1–7 range) in the TRY database (Kühn et al., 2004; Kattge et al., 2011). We used the leaf palatability rating as measure of functional efficiency.

For pest control, we included species reported as consumers of mammal and invertebrate pests in Civantos et al. (2012). We calculated functional efficiency for each species by calculating the percentage of invertebrate and mammal food in their diet (Wilman et al., 2014). The carcass removal providers contained mammal and bird species that rely on scavenging for food (Wilman et al., 2014) and their functional efficiency was calculated based on the percentage of scavenging in their diet. For seed dispersal, we defined as providers the mammals and birds with seeds and fruits in their diet (Wilman et al., 2014). We calculated their functional efficiency as the percentage of seeds and fruits in their diet.

For hunting, we included species that are hunted in Europe (Schulp et al., 2014, data provided by authors), irrespective of their role in nutrition, and we considered for all species a uniform functional efficiency. The existence value providers were defined based on the European Regional Assessments of the Red List. We included species that were assessed as vulnerable, endangered or critically endangered at European level (Bilzet al., 2011; BirdLife International, 2015; Cox and Temple, 2009; Temple and Cox, 2009; Temple and Terry, 2007). Their status was used as an indicator of functional efficiency with the status "vulnerable" receiving the lowest score of one and the "critically endangered" receiving the maximum score of three.

Finally, to define the providers of wildlife watching, we carried out a search on the World Wide Web using Google's Search Engine by using the search string "Wildlife watching in < country>". We used the

English expression because searches in local languages were difficult to process and they produced many results related to non-European wildlife tourism targeting European tourists. We used the common names (e.g. France instead of the official French Republic) of 34 countries within our geographic extent. We searched webpages provided by the first 6 Google search results pages for each country, excluding the advertised web links. We selected the web pages that clearly referred to wildlife watching as a touristic activity and we recorded all species of interest. When species were likely to be listed on another webpage of the respective website, we navigated to that webpage. When referred by the common name, we included only wildlife that could be identified to species level with a reasonable level of certainty. We then pooled the results and summed the recorded species across all countries, resulting in a range between one and 210 records. We used the number of records of wildlife watching as the metric for their functional efficiency.

2.3. *Step 2 – Extracting and stacking the distributions of ES providers*

We collected the geographic distributions of providers from atlas datasets with a grid cells size, henceforth resolution, of 50 × 50 km containing 4174 plants (Lahti and Lampinen 1999), 194 mammals (Mitchell-Jones *et al.,* 1999), 498 birds (Hagemeijer and Blair 1997), 133 reptiles and 70 amphibians (Sillero et al., 2014). In the case of bird species, the data represent occurrences during the breeding period. The geographical extent included the Mediterranean islands but excluded Cyprus. We removed Ukraine, Belarus, Moldova and the European part of Russia where recording effort was less uniform and intense (Williams et al., 2000). The sampling intensity was measured at grid cell level only for the bird dataset and we retained only the cells with the highest completeness of coverage (identification of at least 75% of expected breeding species) (Hagemeijer and Blair, 1997). All datasets except the bird data were compiled in the Common European Chorological Grid Reference System (CGRS) agreed by the groups mapping European biodiversity. For bird species, the data were compiled in the European Ornithological Atlas (EOA) grid at the same resolution. For this dataset, we overlaid the EOA grid with the CGRS grid and we identified the EOA grid cells overlapping each CGRS grid cell. Most of the CGRS cells corresponded clearly to a particular EOA grid cell. Only 28 CGRS grid cells (approximately 1% of our grid) overlapped significantly (more than 1% of their area) with more than one EOA grid cell. In these cases, the EOA cells were usually divided spatially across several CGRS cells. For the 28 CGRS cells overlapping with more than one EOA cell we calculated the coverage of different habitat types according to the EUNIS data (Moss, 2014). We then reassigned the species from the EOA to the CGRS cells by including in the 28 CGRS grid cells all the common species across the overlapping EOA cells and then all the other species whose preferred habitat types covered at least 5% of the CGRS cell area.

2.4. *Step 3 – Weighting and summing of ES providers into WPR*

We calculated for each provider of each species-based ES:

$$W(j,k) = \frac{FE(j,k)}{\max(FE_j))} \tag{1}$$

where W (j, k) was the normalized functional efficiency which weights the contribution of species k to service j, henceforth weighting, *FE(j, k)* was the functional efficiency of species k for service j measured according to the specific metric used for each species-based ES, and max (FE_j) was the maximum functional efficiency recorded for each service.

We then combined the geographical distributions of all providers for each species-based ES in the CGRS system. For each grid cell:

$$WPR_{ij} = \sum\nolimits_{k=1}^{N} S(i,k)^{*}E(j,k)^{*}W(j,k) \tag{2}$$

where *WPR* was the WPR for service *j* in grid cell *i* i.e., weighted provider richness*, S(i, k)* was one when species *k* is present in grid cell *i* or zero otherwise, *E(j, k)* was one when species *k* is a provider of service *j* or zero otherwise, and W (j, k) is the weighting of species k for service j.

2.5. *Step 4 – Normalizing WPR*

We normalized WPR of each species-based ES in each grid cell in two steps.

i) We calculated three adjusted values for WPR according to different hypotheses on the provider richness and the functional efficiency needed for ES. We used the formula:

$$WPRa_{ij} = WPR_{ij}^{a} \tag{3}$$

where *WPRa* is the adjusted WPR for service *j* in grid cell *i*, WPR_{ij} is raw WPR for service *j* in grid cell *i*, and *a* is a constant that modifies the relationship and takes the values 0.2, 1 or 3 for concave, linear and convex relationships, respectively. A concave relationship assumes that most of the service supply is produced at relatively low values of WPR and each new unit of functional efficiency adds a decreasing contribution to ES supply (Kleijn et al., 2015). A convex relationship assumes that a minimum value of WPR is necessary for substantial supply and each new WPR unit adds an increasing contribution (Williams-Guillén et al., 2008). A linear relationship (a = 1) assumes that all units of functional efficiency are equally important for ES supply. We chose these *a* values for the non-linear relationships because they result in steep shapes that delimit a large functional space and, when the resulting values are normalized and summed, we achieve a substantial effect of varying relationships on the aggregated WPR for multiple species-based ES.

ii) In the second step, we normalized the three *WPRa* to the interval [0,1] according to:

$$WPRn_{ij} = \frac{WPRa_{ij} - WPRa_{jmin}}{WPRa_{jmax} - WPRa_{jmin}} \tag{4}$$

where *WPRn* is the normalized WPR for service *j* in grid cell *i*, $WPRa_{ij}$ is the adjusted WPR for service *j* in grid cell *i*, $WPRa_{j\,\min}$ and $WPRa_{j\,\max}$ represent the minimum and maximum of adjusted WPR of service j across all grid cells, respectively.

3. Ecosystem services based on biophysical data

We selected 9 biophysical services for which European-wide data were available (Table S2): cultivated food, cultivated fodder, energy crops, harvested timber, grazing livestock, water retention capacity, soil protection, carbon stocks, recreation potential. Data sources included 8 datasets created for the year 2010 to support the Mapping and Assessment of Ecosystems and their Services (MAES) under Action 5 of the EU Biodiversity Strategy (Maes et al., 2012, 2015; Paracchini et al., 2014) and a global map of carbon stocks for the year 2000 (Ruesch and Gibbs 2008). The MAES data are available at: http://data.jrc.ec.europa.eu/collection/maes. The methods for modeling biophysical services are detailed in the Supplementary information and fully explained in Maes et al. (2012) and Ruesch and Gibbs (2008). For the comparison with WPRs of species-based ES, we aggregated the data from their initial resolutions (Table S3) to the CGRS grid resolution through three methods: average, median value and average of the top 10% values from all spatial units overlapping with each CGRS cell. Finally, we normalized all services to a range from 0 to 1 according to Eq. (4).

4. Analysis

4.1. *Spatial correlation*

We performed correlations between the normalized values of biophysical ES and normalized WPR (WPR_n in the Eq. (4)), henceforth WPR, in several steps, each step increasing by one the number of biophysical ES and WPRs, starting with one each and ending with 9 each. Each step involved a series of procedures. i) To remove potential spatial autocorrelation effects and understand the variation in correlation coefficients, we selected 500 random subsets of 100 grid cells (5%) from those common to all datasets. Each of the 500 selections was performed without replacement from all grid cells with values for all ES and WPRs. ii) For each subset of grid cells, we then sampled a subset of biophysical ES and WPR from one to 9 according to the number considered in each step (i.e., in the first step, we sampled randomly one biophysical ES and one WPR for each subset and used only those values to calculate the correlation for that particular subset; in the second step, we sampled randomly two biophysical ES and two WPRs; and so on until

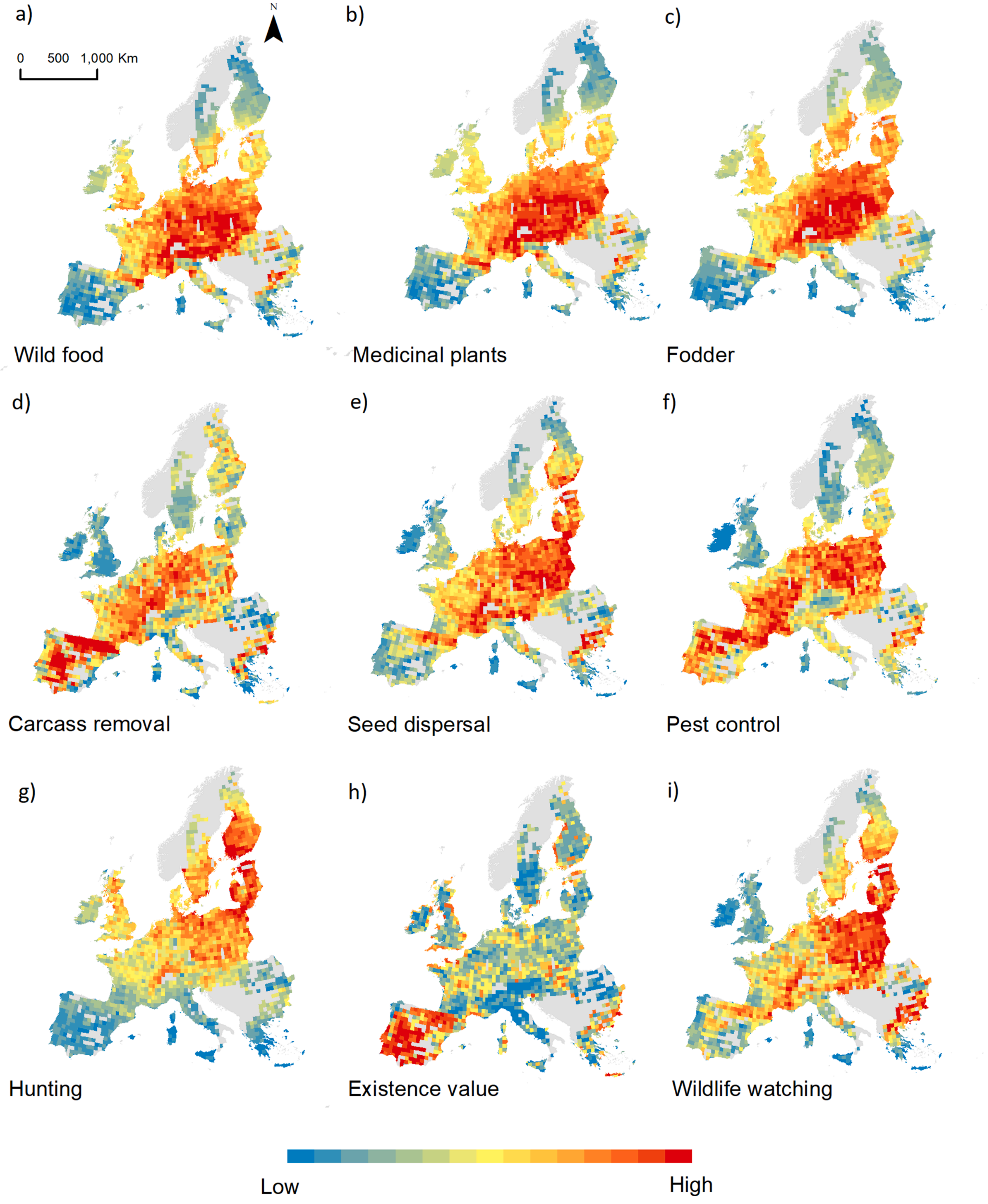


Fig. 1. Weighted provider richness for species-based services at 50 × 50 km resolution. The color categories display quantiles.

the ninth step when all biophysical and WPRs are used for correlation). iii) In the case of WPR, we sampled one of the three possible weighting functions: linear, convex and concave. For biophysical ES, we sampled one of the three aggregation methods: average, median value and top 10% values. iv) Within each cell, we then summed separately the normalized values of biophysical ES and WPR. v) We performed spatial rank correlations between the biophysical ES and WPR for each subset of 100 cells. vi) We calculated the range that included 95% of correlation results (CI 95%) for the 500 subsets of each step. At national scale, we repeated the same steps for each country covered by at least 40 grid cells (not shared with other countries). Instead of 100 grid cells, each random subset included 25% of the cells of the national territory of each country (minimum 10 grid cells for countries covered by the lowest number of grid cells).

4.2. *Synergies and trade-offs*

We analyzed synergies and trade-offs in an approach similar to the

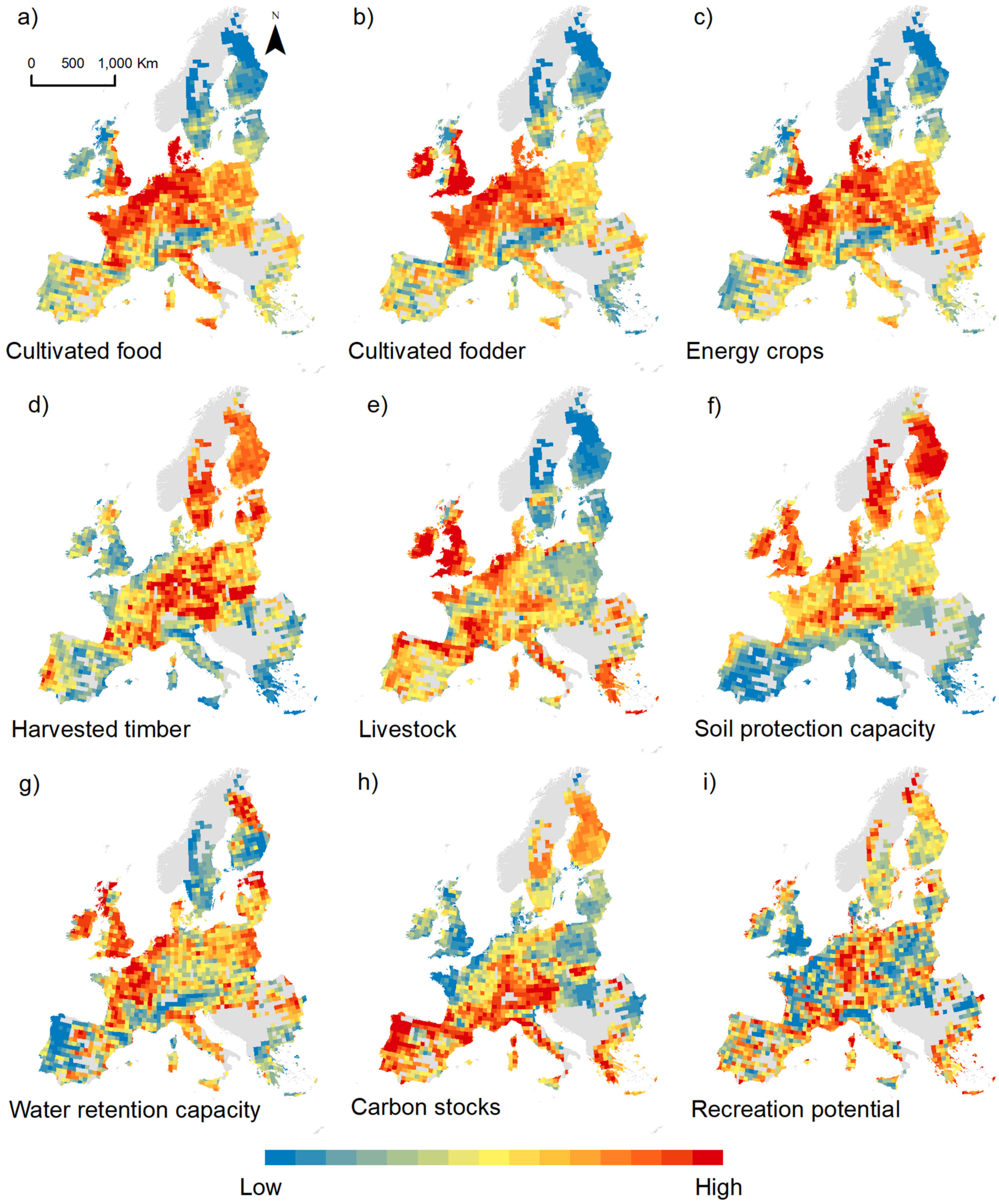


Fig. 2. Spatial distribution of biophysical services at 50 × 50 km resolution. The color categories display quantiles.

spatial correlation procedure. i) For each combination of either biophysical ES or WPRs, we selected 100 random subsets of 100 grid cells for each biophysical ES or WPR. ii) We then performed rank correlations between the two sets of values based on the linear relationship (a = 1 in formula 2) in the case of WPRs and and the mean-based aggregation for the biophysical ES. iii) We calculated the range that included 95% of correlation results (CI 95%). If all values of the CI 95% were above 0, we considered that there was a synergy between the two biophysical ES or WPRs. If all values of the CI 95% were below 0, we considered that there was a trade-off. At national scale, we repeated the same steps for each country by selecting 25% of cells of national territories for each random subset.

5. Results

Weighted provider richness (WPR) for most species-based ES had the highest values in central Europe (Fig. 1). The distribution of wild food, medicinal plants and fodder WPRs were particularly similar due to the importance of plant distribution patterns for each of these species-based ES. Biophysical ES had similar distribution patterns with the highest values in central Europe (Fig. 2). The distribution of crop-based biophysical ES (cultivated food, cultivated fodder and energy crops) were the most similar among the 9 biophysical services.

The correlations between increasing numbers of WPRs and biophysical ES at European scale were either positive or non-significantly different from 0. The distribution of correlation results became narrower with the increase in number of ES (Fig. 3a). The average correlation ranged between 0.15, CI 95% = [−0.27, 0.57], for one biophysical ES and one WPR, and 0.51, CI 95% = [0.36, 0.64], for 9 biophysical ES and 9 WPRs. The CI 95% did not include zero when correlating combinations of at least five biophysical ES and WPRs (Fig. 3). The results at national level varied among the 10 countries retained for analysis . For 5 countries (Spain, UK, Italy, Greece, Finland) the trend was similar to the one at European level, with the correlations becoming increasingly positive with the increase in number of biophysical ES and WPRs. For these countries, the CI 95% became positive when considering at least 4 (Greece), 6 (Spain), 7 (Italy), 8 (UK) and 9 (Finland) biophysical ES and WPRs. For France, Germany, Sweden, Poland and Romania the correlations did not become increasingly positive with the increase in number of ES and WPRs or the trend was not strong enough to lead to positive CI 95% at any number of biophysical ES and WPRs. For example, for Germany the average correlation ranged between 0.02, CI 95% = [-0.48, 0.56], for one biophysical ES and one WPR, and −0.05, CI 95% = [0.43,0.32], for 9 biophysical ES and 9 WPRs.

The choice of weighting function for WPRs did not have an impact on correlations. The patterns held for random assignment of functions (Fig. S4), the concave function (Fig. S5) and cell rankings (Fig. S6). The different aggregation functions for biophysical ES also exhibited few differences (Figs. S2 and S3).

We identified trade-offs at European scale between most provisioning biophysical ES on one hand, and regulating and cultural services on the other (Fig. 4a). Among the provisioning ES, only harvested timber had synergies with soil protection and carbon stocks while cultivated food, fodder and energy crops had synergies with water retention. WPRs were mostly positively correlated with each other at European scale, indicating strong synergies between providers of different species-based ES (Fig. 4b). The strongest synergies were those between wild food and medicinal plants (0.98, CI 95% 0.96–0.98), medicinal plants and wild fodder (0.94, CI 95% 0.92–0.96), and wild fodder and wild food (0.93, CI 95% 0.89–0.95). The pairs of WPRs that did not have synergistic relations were existence value and medicinal plants, existence value and wild food, existence value and wild fodder, and existence value and hunting. Hunting had weak synergies with carcass removal (0.23, CI 95% 0.05–0.39) and pest control (0.23, CI 95% 0.09–0.35) as did seed dispersal and existence value (0.19, CI 95% 0.04–0.34). However, at national scale the patterns differed (Figs. S7 and S8). While in France all WPRs were synergistic with each other but two pairs (existence value vs. wild fodder and medicinal plants), in Poland 16 pairs of WPRs were not synergistic (Fig. S8). For biophysical ES, the relationships were also different at continental and national scales. For example, water retention's synergies with provisioning ES at European scale became a trade-off in Finland and a neutral relationship in the UK (Fig. S7).

6. Discussion

The similarities and differences in spatial patterns between biophysical ES and species-based ES at large scales have gone unexamined in the literature (but see Roussel et al., 2017 for a fine scale study). We show here that biophysical ES generally correlate positively at European scale with weighted provider richness (WPR) and that correlation coefficients increase with the number of biophysical ES and WPRs. At national scale, the relationship between biophysical ES and WPRs tends to be positive in half of the countries and neutral in the other half. The synergies and trade-offs of WPRs are different from those of biophysical

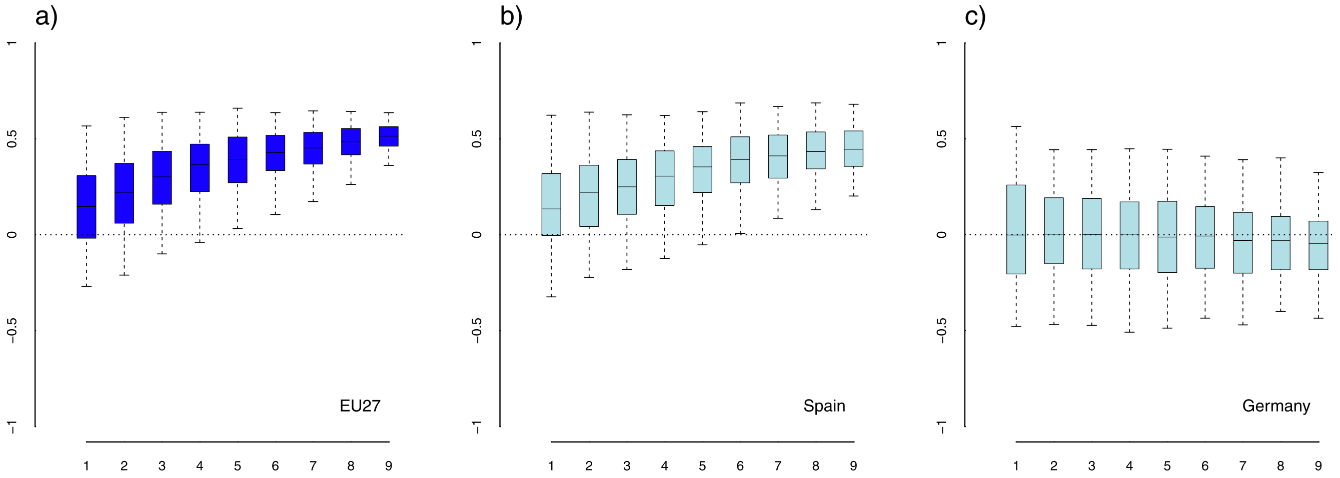
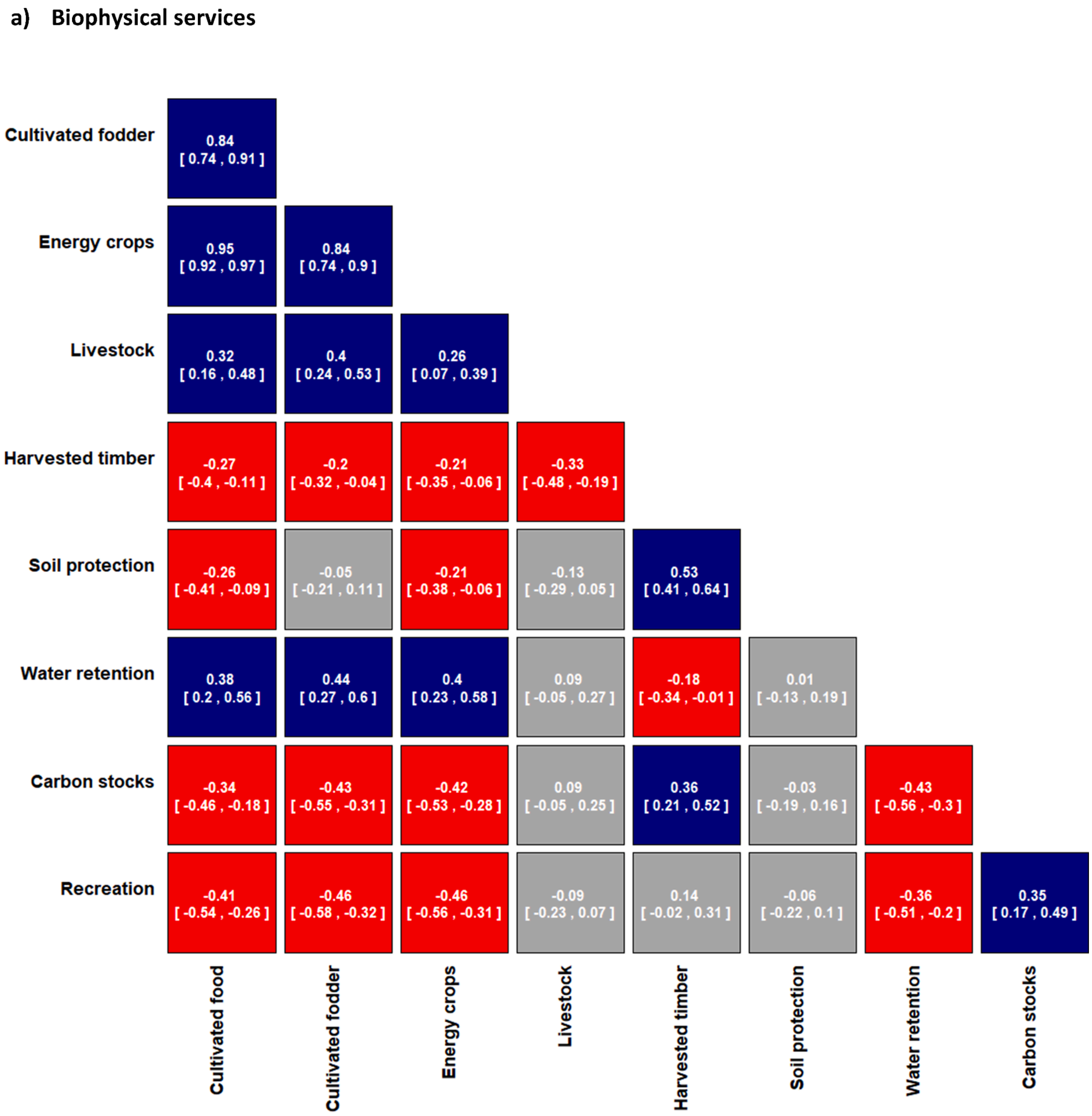


Fig. 3. Results of rank correlations between biophysical services and weighted provider richness for species-based services for a) the European Union in 2007 with 27 members (EU27), and two countries showing the difference in correlation patterns at national level: b) Spain and c) Germany. The results for all countries are available in Fig. S4. Each box represents 500 spatial rank correlations calculated based on random subsets of grid cells. The black band inside each box represents the median, the boxes represent 50% of values around the median, and the whiskers extend to 95% of the correlation values around the median. The dotted line indicates 0.



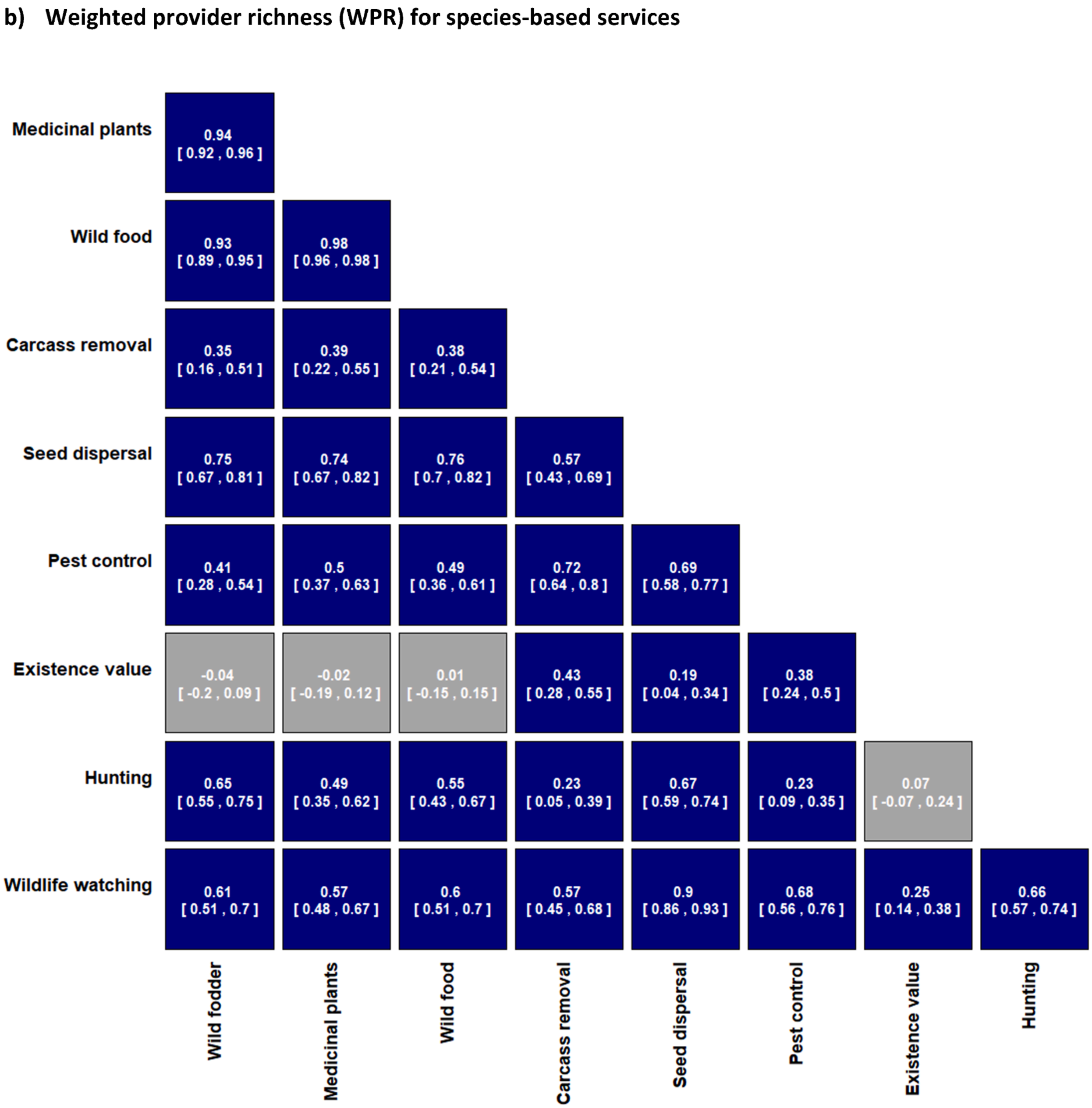
a) Biophysical services

	Cultivated food	Cultivated fodder	Energy crops	Livestock	Harvested timber	Soil protection	Water retention	Carbon stocks
Cultivated fodder	🟦 0.84 [0.74 , 0.91]							
Energy crops	🟦 0.95 [0.92 , 0.97]	🟦 0.84 [0.74 , 0.9]						
Livestock	🟦 0.32 [0.16 , 0.48]	🟦 0.4 [0.24 , 0.53]	🟦 0.26 [0.07 , 0.39]					
Harvested timber	🟥 -0.27 [-0.4 , -0.11]	🟥 -0.2 [-0.32 , -0.04]	🟥 -0.21 [-0.35 , -0.06]	🟥 -0.33 [-0.48 , -0.19]				
Soil protection	🟥 -0.26 [-0.41 , -0.09]	⬜ -0.05 [-0.21 , 0.11]	🟥 -0.21 [-0.38 , -0.06]	⬜ -0.13 [-0.29 , 0.05]	🟦 0.53 [0.41 , 0.64]			
Water retention	🟦 0.38 [0.2 , 0.56]	🟦 0.44 [0.27 , 0.6]	🟦 0.4 [0.23 , 0.58]	⬜ 0.09 [-0.05 , 0.27]	🟥 -0.18 [-0.34 , -0.01]	⬜ 0.01 [-0.13 , 0.19]		
Carbon stocks	🟥 -0.34 [-0.46 , -0.18]	🟥 -0.43 [-0.55 , -0.31]	🟥 -0.42 [-0.53 , -0.28]	⬜ 0.09 [-0.05 , 0.25]	🟦 0.36 [0.21 , 0.52]	⬜ -0.03 [-0.19 , 0.16]	🟥 -0.43 [-0.56 , -0.3]	
Recreation	🟥 -0.41 [-0.54 , -0.26]	🟥 -0.46 [-0.58 , -0.32]	🟥 -0.46 [-0.56 , -0.31]	⬜ -0.09 [-0.23 , 0.07]	⬜ 0.14 [-0.02 , 0.31]	⬜ -0.06 [-0.22 , 0.1]	🟥 -0.36 [-0.51 , -0.2]	🟦 0.35 [0.17 , 0.49]

Fig. 4. Synergies and trade-offs for a) biophysical services and b) weighted provider richness (WPR) for species-based services at European scale. Blue rectangulars indicate synergies between ES or WPRs (CI 95% of correlation results above 0), red rectangulars indicate trade-offs (CI 95% of correlation results below 0), grey rectangular indicate a neutral relationship (the CI 95% of correlation results includes 0). The numbers in each rectangular show the average and the range of the confidence interval at 95%. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ES, with provisioning WPRs being mostly synergistic with regulating and cultural WPRs. Therefore, the inclusion of species-based ES in large-scale assessments, for which WPRs are a first step, will lead to a more nuanced discussion of ES spatial patterns, trade-offs and synergies than allowed by current large-scale assessments focused on biophysical ES. For example, while cultivated fodder presents trade-offs with many regulating and cultural services, WPR for wild fodder is synergistic with many other WPRs, potentially leading to different decisions related to grain-fed and grass-fed cattle (Eshel et al., 2018). The inclusion of species-based ES in large scale ES assessments will also make explicit the contribution of biodiversity to multiple ES, nuancing our understanding of how land cover contributes to ES. For example, large-scale tree planting for carbon sequestration (Bastin et al., 2019) was criticized for implying the afforestation of many natural grasslands, which are habitats for many providers of other ES (Veldman et al., 2019). Making biodiversity contribution explicit can also support better decision-making in restoration projects. The Green for Grain restoration program in China has achieved great benefits in terms of reducing soil erosion but the choice of non-native species for afforestation has led in some cases to decreases in ES supported by native species (Cao et al., 2009).

Scale leads to variation in spatial patterns, synergies and trade-offs for both biophysical ES and WPRs. Our results confirm previous studies highlighting the importance of scale for spatial patterns of ES (Verhagen et al., 2017; Cimon-Morin and Poulin, 2018; Hou et al., 2018) and biodiversity (Kukkala et al., 2016). Extent is particularly relevant in



b) Weighted provider richness (WPR) for species-based services

	Wild fodder	Medicinal plants	Wild food	Carcass removal	Seed dispersal	Pest control	Existence value	Hunting
Medicinal plants	0.94 [0.92 , 0.96]							
Wild food	0.93 [0.89 , 0.95]	0.98 [0.96 , 0.98]						
Carcass removal	0.35 [0.16 , 0.51]	0.39 [0.22 , 0.55]	0.38 [0.21 , 0.54]					
Seed dispersal	0.75 [0.67 , 0.81]	0.74 [0.67 , 0.82]	0.76 [0.7 , 0.82]	0.57 [0.43 , 0.69]				
Pest control	0.41 [0.28 , 0.54]	0.5 [0.37 , 0.63]	0.49 [0.36 , 0.61]	0.72 [0.64 , 0.8]	0.69 [0.58 , 0.77]			
Existence value	-0.04 [-0.2 , 0.09]	-0.02 [-0.19 , 0.12]	0.01 [-0.15 , 0.15]	0.43 [0.28 , 0.55]	0.19 [0.04 , 0.34]	0.38 [0.24 , 0.5]		
Hunting	0.65 [0.55 , 0.75]	0.49 [0.35 , 0.62]	0.55 [0.43 , 0.67]	0.23 [0.05 , 0.39]	0.67 [0.59 , 0.74]	0.23 [0.09 , 0.35]	0.07 [-0.07 , 0.24]	
Wildlife watching	0.61 [0.51 , 0.7]	0.57 [0.48 , 0.67]	0.6 [0.51 , 0.7]	0.57 [0.45 , 0.68]	0.9 [0.86 , 0.93]	0.68 [0.56 , 0.76]	0.25 [0.14 , 0.38]	0.66 [0.57 , 0.74]

Fig. 4. (*continued*).

land planning for entities such as the EU, which has biodiversity policies (Council of the EU, 1979) and implementation mechanisms (European Commission, 2013) at different administrative levels from municipal to supra-national (Kark et al., 2009; Montesino Pouzols et al., 2014). This creates potential for conflict between administrative levels and more research should be conducted on how mapping at different extents and resolutions can improve decision-making. For example, the data used here are an indication of regional species pools at the scale of large subnational units (i.e., NUTS 2 and NUTS 3, EUROSTAT, 2011) but ES supply depends on species presence and abundances at fine scales (Karp et al., 2013). High WPR for wild food and medicinal plants in regional species pool can represent arguments for habitat conservation to encourage local economies based on these wild products (Cerqueira et al., 2015) but zoning of protected areas for ES should be based on biodiversity data at fine resolutions (Ceaușu et al., 2015). Moreover, species conservation or ES that have benefits at large scales, such as carbon sequestration, are more effectively managed through planning at large extents while ES experienced at local scales should be conserved and managed at the level of small administrative units (Verhagen et al., 2017).

7. Limitations and further steps

Our results should be considered in the context of several data limitations. In the case of biophysical ES, the quantity and quality of estimates differed between countries and, in some cases, within countries (Maes et al., 2015). Although remote sensed data and other biophysical datasets have a relatively high consistency and reliability, it is important to avoid overconfidence in what the biophysical models of ES tell us. For example, the spatial patterns of water regulation (Maes et al., 2011) can be quite different from the spatial patterns of the water retention index (Maes et al., 2015) used here, all depending on the choice of biophysical model. Moreover, remote sensed data such as land cover maps often lack information on ecological contexts, missing the difference, for example, between natural forests and plantation forests (Hansen et al., 2013).

In terms of biodiversity data, although European atlases are among the most complete datasets at continental level, there are still substantial gaps. For example, the plant data included here contains only approximately 20% of the European flora (Ronk et al., 2015) and some reported species are also cultivated. Despite the Mediterranean basin being recognized for high levels of plant diversity and endemism, this dataset (Fig. S1) indicates for this region a species richness similar to that of northern Europe, although Ronk et al. (2015) concludes that variation in plant diversity is overall well represented at continental scale. In the case of amphibians and reptiles, data compilation was hindered by different approaches to data-sharing across Europe (Sillero et al., 2014). Atlas data also require a long time to collect and compile, frequently lack any information on species abundances and use a coarse resolution (Greenwood 2017). In our case, measures of sampling completeness are only available for birds and uniform quality control is difficult over such large areas. Moreover, atlas data for other important service provider taxa (e.g., insects) are unavailable, which made it impossible for us to map certain species-based ES such as pollination. The long time needed to compile the atlas datasets (Greenwood 2017) and, to a lesser extent, the biophysical data, limit their usability for decision-making. Future mapping of species-based ES would strongly benefit from use of technologies and methods that speed up data availability and reduce these time lags.

The quality and quantity of biodiversity data represents the main limitation in mapping species-based ES and represents the priority for future efforts. To correct the coarse resolution of atlas data, Civantos et al. (2012) used species distribution models to map pest control. These models are useful for answering specific research questions but they do not capture species interactions and non-climatic distribution constraints (Sinclair et al., 2010; Guillera-Arroita et al., 2015; Jarnevich et al., 2015), which can reduce their effectiveness in estimating species-based ES. The recent trend towards large data syntheses can provide opportunities for species-based ES mapping. For example, Kleijn et al. (2015) and Winfree et al. (2018), and (Karp et al. 2018) compiled large datasets from local-scale pollination studies and pest control studies, respectively. Their analyses provide insights unparalleled for other species-based ES, especially in the case of pollination. These studies can serve as a model for other species-based ES but so far this type of analysis has not been replicated for other species-based ES. Another important limitation is represented by insufficient knowledge on functional efficiency of taxa for species-based ES across space and time. As Kremen (2005) indicates, functional efficiency of a species can depend on the abiotic environment, resources and community composition among other factors. For example, Mateo-Tomás et al. (2017) show how the species efficiency in carcass removal can change depending on community composition. Characterizing it through a single number as we do here is a rough estimation of a metric that ideally should include a mean and variance to characterize a provider species (Kremen 2005).

The overall importance of a taxon for ES is also dictated by its abundance, a biodiversity metric more difficult to measure at large scales than species presences. With the exception of large data syntheses efforts (Hudson et al., 2017), data on species abundances at large scales are extremely rare. However, new technologies promise progress in this area. For example, remote sensing can support species identification, especially of plants (Pettorelli et al., 2014), which can then help to calculate abundances. Environmental DNA (Bohmann et al., 2014) and camera trapping (Rich et al., 2016) also provide hope that concerted efforts for biodiversity monitoring can address data limitations for species-based ES in the foreseeable future (Pereira and Cooper 2006).

Understanding functional efficiency and abundances across time and space can finally lead to a better understanding of the functional relationships between provider richness and species-based ES supply. The functional relationship will likely vary widely across time and space beyond the three functional shapes that we use here. For now, the existing knowledge is largely limited to pollination, and, to a lesser extent, carcass removal, pest control and wildlife watching (Perfecto et al., 2004; Booth et al., 2011; Mateo-Tomás et al., 2017). For some species-based ES such as wild food, abundance might play a bigger role in supply than in others, such as in wildlife watching, where the diversity of providers might be most important. In other cases, such as carcass removal, both diversity and abundance might play a role in different ecological contexts (Mateo-Tomás et al., 2017).

8. Conclusion

The use of the term “ecosystem services” in large-scale ES assessment has so far mainly referred to biophysical ES. Failure to include information on species-based ES means that these assessments will continue to provide incomplete knowledge on the role of biodiversity, and the spatial patterns beyond those observed in biophysical ES. This is not an outcome we can afford considering the accelerated environmental change we are experiencing. We call here for increased efforts for a balanced assessment of the entire range of ES in parallel with research on the relationship between ES, provider richness and functional efficiency. Initiatives such as the regional and global assessments led by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) provide an excellent opportunity to develop such initiatives that cover both species-based and biophysical ES.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoser.2021.101259.

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