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Assessing the distribution of forest ecosystem services in a highly populated Mediterranean region

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ABSTRACT

Forest ecosystems provide a wide range of goods and services to society and host high levels of biodiversity. Nevertheless, forest ecosystem services (ES) are often quantified and assessed using simplified methodologies (e.g., proxy methods based exclusively on Land Use Land Cover maps) that introduce substantial uncertainty in the analysis by ignoring, for instance, the species composition and spatial configuration of the ecosystems studied. In this work we defined and calculated a set of 12 indicators of several ES for the forests of the highly populated region of Catalonia (North-eastern Iberian Peninsula). The indicators combined different sources of information such as forest surveys, ecological model predictions and official statistics, but also included additional land cover information. All ES indicators were aggregated at the municipality level to compare their values and distribution patterns. We assessed spatial trade-offs and synergies among ES, as well as their relationships with a set of socioeconomic, climatic and biodiversity variables using correlation analyses and mixed-effects models. The results suggest a clustering of provisioning and regulating ES in mountainous zones towards the North of the study area. These two types of services showed a high degree of spatial similarity and presented high positive correlations. In contrast, cultural ES showed a more scattered pattern, which included lower elevation areas in the South of the study region. Climatic conditions were the main determinants of the spatial variability in the supply of the different ES, with most indicators being positively associated with precipitation and negatively associated with temperature. In addition, biodiversity (particularly woody species richness) showed positive relations with most of these ES, while socioeconomic variables (such as population density and the percentage employment in agriculture) showed negative associations with most of them. The combination of information from different data sources (including primary data) allowed for a detailed analysis of forest ES, likely removing some of the problems derived from approaches based only on proxy methods. In addition, the use of municipalities as study unit makes results directly relevant to management and planning strategies operating at this scale (e.g., forest management and planning).

1. Introduction

Forest ecosystems are key elements for the maintenance of global biodiversity (Brooks et al., 2006). They support a range of ecosystem functions and provide multiple and essential ecosystem services (ES) to society (MEA, 2005). Some of the main forest ES can be classified as regulating services: climate and water regulation, erosion and flood control, etc. (Miura et al., 2015). However, materials and energy provision and cultural services are also relevant in forests (MEA, 2005). Forest ecosystems have been strongly disturbed and modified by the human use of the landscapes, although the intensity of historical disturbances and the current condition of these ecosystems are highly heterogeneous in space (FAO, 2014; Trumbore et al., 2015).

Several authors have highlighted the relevance of the biodiversity

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contained in Mediterranean landscapes (Brooks et al., 2006) and in particular in the Mediterranean Basin (Medail and Quezel, 1999; Hampe and Petit, 2005), which is considered a biodiversity hotspot of global relevance (Myers et al., 2000). The forests of this region have been managed and modified for millennia due to the historical use of natural resources by human societies (Underwood et al., 2009). In the context of global change, the development of effective management and conservation strategies is key for the maintenance of their diversity and ecosystem functions (Costanza et al., 1997). A series of drivers have been identified as having potential effects on forest ecosystems and their supply of ES (EME, 2011; Thom and Seidl, 2016), including land-use changes, wildfires, climate change, alien species, pests and pathogens (Vila et al., 2010; Doblas-Miranda et al., 2015).

Methodological factors may have a large impact on the quantification of ES (Eigenbrod et al., 2010; Van der Biest et al., 2015) and are important sources of uncertainty in ES assessments (Hou et al., 2013). Land Use/Land Cover (LULC) information often constitutes the basis for ES assessments (Hou et al., 2013). However, the use of proxy-based methods relying only on LULC data assumes that if one class (an ecosystem type) provides a specific ES, the level of supply is constant in space, neglecting the importance of other ES drivers not represented by land use categories. This leads to a potentially large generalization error in ES assessments (Plummer, 2009). Notably, these proxy-based approaches often hide large differences in the composition and structure of the forests that drive ecosystem functioning (Vila et al., 2007; Ruiz-Benito et al., 2014) and ES supply (Alamgir et al., 2016; Sutherland et al., 2016). Recent studies overcome some of the limitations of proxy-based methods by defining specific bio-physical indicators (Rodríguez-Loinaz et al., 2015) or by using specific information about the structure and the composition of these ecosystems (Roces-Díaz et al., 2017). Finally, accurate assessments of ES should include the analysis of ES spatial patterns and their spatial associations (Andrew et al., 2015), including synergies and trade-offs as well the identification of areas with particularly high levels of overall supply (hotspots; Mouchet et al., 2014; Schröter and Remme, 2016).

Forest planning and management strategies are beginning to include forest ES as key elements in their assessments (e.g. Frank et al., 2015; Triviño et al., 2015), which can help to visualize and promote the multifunctionality of these systems. Spatial-dependent aspects, such as the scale and the administrative level of analysis, become particularly relevant for planning and management objectives (Hein et al., 2006). In this regard, the municipal domain often offers a good compromise between reasonable spatial resolution and administrative relevance (Rodríguez-Loinaz et al., 2015; Roces-Díaz et al., 2018). Within this management-oriented perspective, the spatial patterns and relationships between ES (trade-offs and synergies) should also be evaluated (Duncker et al., 2012). For instance, negative relationships are frequently reported among materials provision (such as timber) and cultural services (García-Nieto et al., 2013) or biodiversity (Duncker et al., 2012).

In recent years several studies have analysed the ES provided by European Mediterranean landscapes and uncovered their strong relations with social and environmental characteristics (Garcia-Llorente et al., 2015). Some of these studies have focused on the assessment of specific, particularly relevant ES such as water provision (Quintas-Soriano et al., 2014) or erosion regulation (Guerra et al., 2016), while other works have described and analyzed all the ES provided by specific types of forest ecosystems (e.g., cork oak woodlands (Bugalho et al., 2011)). However, there are still few studies addressing different forest types at the regional scale and including a complete set of ES as a necessary step to address trade-offs and spatial variability in their overall provision (but see García-Nieto et al., 2013).

In this work we define a comprehensive set of bio-physical indicators of forest ES for Catalonia (North-eastern Spain) on the basis of different data sources, and assess them at the municipality level. The specific objectives of this work are: i) to analyze the spatial patterns of these ES and to identify their main hotspot areas; and ii) to assess the spatial relationships of these ES (trade-offs and synergies) and the association between these ES and different socioeconomic, climatic and biodiversity variables that characterize the study area. We hypothesize that the ES analyzed will show clearly differentiated spatial patterns, with a high clustering of provision and regulating services on mountainous municipalities with higher forest cover and lower population density. Other ES (e.g., cultural) will be associated to more populated areas. These disjoint spatial patterns may reflect trade-offs between different ES.

2. Material and methods

2.1. Study area and outline of the experimental approach

Our study area is Catalonia (North-eastern Spain; Fig. 1), an administrative region that covers 32,114 km^2. It is mainly located in the Mediterranean Biogeographic Region, although a part of its northern area (the Pyrenees Mountains) belongs to the Alpine Region. It is a mountainous area with an altitudinal range from the sea level to more than 3000 m on the highest peaks of the Pyrenees. Catalonia had a population of 7,504,008 people in 2015, 43% of them concentrated in the metropolitan area around the capital city (Barcelona, 636 km^2). It is a highly forested region (43% of its area was covered by forest; LCMC, 2009) where about 33% of the land area was included in the Natura 2000 Network (a system of nature protection areas in the territory of the European Union). It is dominated by tree species of the Pinaceae and Fagaceae families. Forests from coastal and low altitude areas are dominated by *Pinus halepensis* Mill. (Aleppo pine), *Quercus faginea* Lam. (Portuguese oak) and *Quercus ilex* L. (Holm oak). At middle-altitude ranges (from 800 to 1500 m) the main species are *Pinus sylvestris* L. (Scots pine), *Pinus nigra* J.F. Arnold (Black pine), *Quercus pubescens* Willd. (Downy oak, synonym of *Quercus humilis* Mill.) and also *Fagus sylvatica* L. (European beech) in the wettest zones. Finally, at altitudes higher than 1500 m the main species are *Pinus uncinata* Raymond ex A.DC. (Mountain pine) and *Abies alba* Mill. (Silver fir). These forests have shown expansion and shrinkage processes over the last millennia in congruence with changes in the environmental conditions on the Mediterranean Basin and historic land use (Grove and Rackham, 2003). Importantly, recent episodes of forest decline have been detected in the study area, affecting mostly species reaching the southern limit of their distribution in the Iberian peninsula, such as *P. sylvestris* (e.g., Martínez-Vilalta and Piñol, 2002) and *F. sylvatica* (e.g., Peñuelas and Boada, 2003). Approximately 80% of the forests in Catalonia are privately-owned, whereas the remaining 20% are public.

The spatial unit of our analysis was the municipality (N = 947 municipalities in Catalonia). ES maps were obtained at this municipality level (see below), where values from different sources (including raster format) were aggregated to polygons. As we focused on forest ecosystems and on ES capacity or actual supply (not demand), we restricted our analyses to those municipalities with substantial forest cover. Thus, we selected only those municipalities that contained at least three permanent plots of the Third National Forest Inventory of Spain (NFI; MAGRAMA, 1997–2007), which was considered a minimum sample size to obtain representative estimates and perform statistical comparisons. The Spanish NFI is an intensive program of periodic surveys (every ∼10 years) that cover the whole forested area of Spain following a uniform sampling design (Appendix S1). Data of the 3rd NFI, conducted in Catalonia in 2000–2001, is used unless otherwise stated. NFI plot density is ∼1 plot/km^2 of forest, so that the 3 plot threshold corresponds with an average of (at least) 300 ha of forest per municipality, resulting in a subset of 576 municipalities. Forest cover ranged between 10% and 95% in these municipalities.

In addition to using NFI data to delineate the areas (municipalities) of interest to this study, we also used the NFI dataset as a basis for the assessment of most ES. The majority of ES indicators were calculated

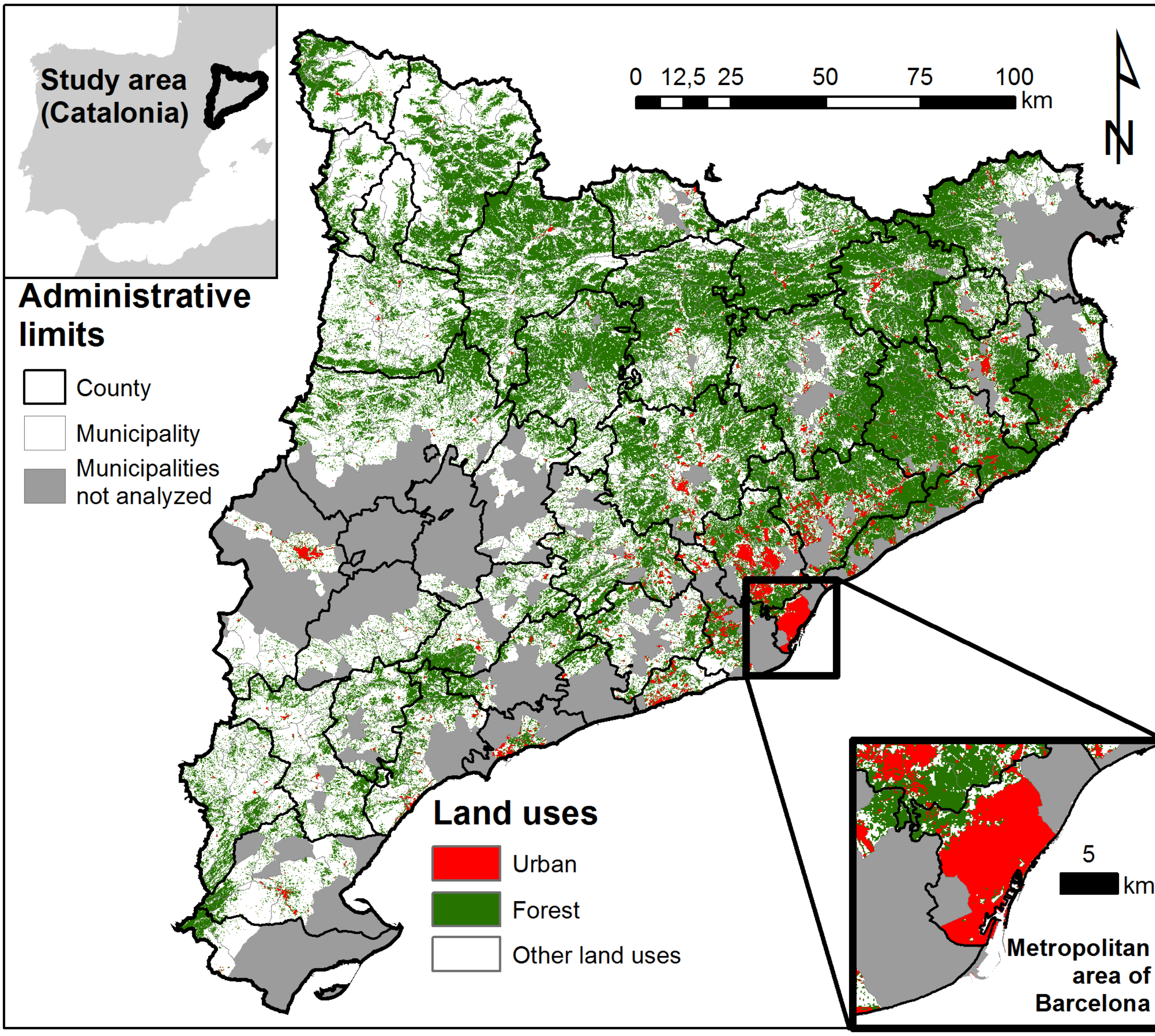

Fig. 1. Location of the study area, distribution of the main types of land uses and location of the metropolitan area of Barcelona, together relevant administrative units as counties and municipalities (source: LCMC, 2009).

either directly from NFI data (NFI data, Table 1) or modelled using primary NFI data as input (model-based). These indicators were calculated for individual NFI plots and then aggregated at municipality level. Other ES were estimated based on combing datasets at municipality level, including aerial photo interpretation and GIS analysis (map-based), official statistics, and additional information provided by research centres or other institutions (other statistics) (Table 1). The resulting ES maps were then aggregated to municipal units and resulting values were compared to explore potential trade-offs and synergies between pairs of ES. Finally, we assessed to what extent climatic and socioeconomic conditions explained the spatial variability of forest ES in the study area. These methods are developed in the following sections.

2.2. Ecosystem services assessment

2.2.1. Bio-physical indicators and ecosystem services typology

For this work we defined a specific set of ES indicators adapted for forest ecosystems of the study area and based on widely used ES classifications (i.e. CICES 4.3: Haines-Young and Potschin, 2013). We considered three categories of ES: provisioning, regulating and cultural. For each category we defined different indicators that are related with the supply (actual or capacity) of specific ES. This set of indicators was developed selecting important forest ES in the study area subject to data availability (see below) and, although it is not exhaustive, it is representative of a wide range of ES. All these indicators are presented in Table 1, while further descriptions of data sources and calculation processes are provided in the Supplementary Material (Appendix S1). Although most indicators defined in this assessment represent actual supply of ES, for three of them there was no available data of actual supply and thus their values represent supply capacity (Table 1).

2.2.1.1. Provisioning category (three ES). We used edible mushrooms production for food provision (P1), as mushroom picking is an important social and economic activity in the study area (Bonet et al., 2010). We estimated edible mushroom production for year 2013 for each municipality in kg/ha/year. For pine forests we combined Third National Forest Inventory (NFI) data and the model developed by de-Miguel et al. (2014). This model accounts for the effects of stand composition, structure and site characteristics in a typical year

Table 1
Description of the ES indicators, their definitions and the units, transformations, sources and temporal ranges used in this work.

ES	Indicator	Code	Definition	Units	Supply	Method used	Transformation	Sources*	Time period
Provisioning									
Food provision	Mushrooms production	P1	Expected edible mushroom production for pine, oak and fir forests in one typical year	kg/ha/year	Capacity	Model-based	ln(X + 0.1)	de Miguel et al. (2014)	2013
Materials/Energy provision	Timber and firewood	P2	Wood extractions and firewood harvesting in public and private forests at municipal level per year	t/ha/year	Actual	Official statistics	ln(X + 0.001)	Generalitat de Catalunya (2014)	2006–2014
Water provision	Exported water	P3	Water exported yearly by surface runoff or deep drainage into the water table for each forest plot (National Forest Inventory, NFI3) in Catalonia	l/m^2/year	Capacity	Model-based	ln(X)	De Cáceres et al. (2015)	1999–2010
Regulating									
Climate regulation	Forest Carbon sink	R1	Forest carbon sink on the above and below ground vegetation	t/ha/year	Actual	NFI data	–	MAGRAMA (1997–2007)	1990–2001
Soil fertility regulation	Soil Organic Carbon	R2	Amount of organic carbon in the soil	t/ha	Actual	Model-based	Sqrt(X)	Doblas-Miranda et al. (2013)	1975–2007
Water regulation	Canopies and soil water storage capacity	R3	Sum of canopy water storage capacity and soil water holding capacity for each forest plot (NFI3) in Catalonia	l/m^2/year	Actual	Model-based	ln(X)	De Cáceres et al. (2015)	1999–2010
Flood protection	Riparian forest cover	R4	Riparian forest cover around watercourses considering a buffer zone of 25 m around	%	Actual	Map-based	Sqrt(X)	LCMC (2009)	2009
Erosion control	Erosion control	R5	Forest cover of areas with a slope higher than 30%	%	Actual	Map-based	Sqrt(X)	LCMC (2009)	2009
Cultural									
Recreational	Rural tourism	C1	Number of beds in rural tourism establishments per municipality	N° places/ha	Actual	Official statistics	Sqrt(X)	IDESCAT (2015)	2014
Existence	Natura 2000	C2	Surface of protected areas included in the Natura 2000 Network.	%	Capacity	Map-based	Sqrt(X)	Generalitat de Catalunya (2015)	2014
Experiential use of organisms	Animal observations	C3	Animal species observations introduced at web portal Ornitho.cat	N° obs./ha/year	Actual	Other statistics	ln(X + 0.0001)	ICO (2014)	2010–15
Physical use of landscape	Wikiloc tracks	C4	Routes recorded in Catalonia and introduced by users at the Wikiloc® app and web portal	N° tracks/ha	Actual	Other statistics	ln(X + 0.001)	Wikiloc®	2006–2014

*The different data sources referenced in this table are more detailed in the Supplementary Material (Appendix S1).

(Appendix S1). Pine forests are by far the most important forests in terms of cover and, particularly, mushroom production in the study area (Bonet et al., 2010). By contrast, for *Quercus* sp. and *A. alba* forests we used their mean production value per unit of forest area (J.A. Bonet, unpublished) because predictive models based on plot characteristics have not been yet developed. For materials and energy provision (P2) we used the annual timber and firewood removals from both public and privately-owned forests for the period 2006–2014 (in t/ha/year). This information was obtained from official statistics provided by the Catalan Government. Finally, for water provision (P3) we used the amount of water exported from forests, estimated as the sum of surface runoff and deep drainage into the water table for each NFI plot (in l/m^2/year). Both quantities were estimated using a soil water balance model (De Cáceres et al., 2015). This model calculates daily water balance driven by meteorological data and additional variables characterizing the soil and vegetation structure. Exported water was estimated for year 2010. More detailed information about this model can be found in Appendix S1.

2.2.1.2. Regulating category (five ES). For climate regulation (R1) we considered the forest Carbon sink capacity in t/ha/year. This value was calculated from the forest Carbon stock change (above- and belowground) using the methodology described in Vayreda et al. (2012) from consecutive forest surveys (comparing plot-level data from 1989–1990 (2nd NFI) and 2000–2001 (3rd NFI)). We used the soil organic carbon (SOC, t/ha) to represent the maintenance of soil fertility (R2), as obtained from the map developed by Doblas-Miranda et al. (2013). The capability of forests to regulate water flows (water regulation, R3) was estimated using the sum of canopies' water storage capacity and soil water holding capacity for each NFI3 plot in l/m^2/year. It was obtained from the same soil water balance model mentioned above (De Cáceres et al., 2015). Flood protection (R4) and erosion control (R5) are strongly dependent on the occurrence of a specific type of ecosystem (riparian forest) or on the detailed distribution of forest cover. For their calculation we used a highly detailed LULC map of Catalonia (LCMC, 2009) with a very high spatial resolution (scale 1:5000 and minimum mapping unit of 500 m^2). For flood protection we used the percentage of area alongside water courses covered by riparian forests. To estimate this coverage, we defined a 25 m buffer around watercourses using the LCMC (2009), and calculated the percentage of riparian forests inside this buffer area. Finally, erosion control was assessed by the percentage of slopes steeper than 30% grade that were covered by forests.

2.2.1.3. Cultural category (four ES). As a proxy of recreational use (C1), we used the number of beds in rural accommodation establishments according to the Official Guide of Touristic Establishments of Catalonia for year 2015 (IDESCAT, 2015), aggregated by municipalities. Existence of landscapes or organisms with conservation interest (C2), was defined as the percentage of municipal surface occupied by protected areas included in the Natura 2000 Network (www.mediambient.gencat.cat). 59.3% of the Natura 2000 Network in the municipalities studied correspond to forests ecosystems. Regarding experiential use of organisms by people (C3) we have calculated the number of animal observations per hectare of municipality using the data stored in the web portal www.ornitho.cat. This portal stores more than 3,000,000 observations (mostly birds but also mammals, reptiles, amphibians and some groups of invertebrates) from more than 3500 observers, and includes species based on the perceived interest by the observer (regardless of ecological functionality or any other 'objective' measure of importance). Data were provided by the Catalan Ornithological Institute (ICO) and represent observations uploaded by users of the application all around Catalonia between 2010 and 2015 (including all its municipalities). Finally, in relation to the physical use of the landscape (C4) we calculated the density of routes per municipality introduced in the web portal www.wikiloc.com, as provided by Wikiloc® (unpublished). Routes include trekking, biking, skiing, running and all types of outdoor routes recorded in Catalonia between 2006 and 2014.

2.2.2. Socioeconomic, climatic and biodiversity predictors of ES supply

We used a series of socioeconomic, climatic and biodiversity variables to assess if they explained ES variability among municipalities. Socioeconomic variables were obtained from the data provided by the regional administration (Statistical Institute of Catalonia: www.idescat.cat, IDESCAT, 2015), aggregated at the municipality level. We considered six socioeconomic variables: population density (inhabitants/km^2), unemployment rate (calculated as the number of unemployed people over the total working population), and the percentage of working population occupied in agriculture, industry, construction and tertiary sector (separately). In addition, we included climatic (mean annual temperature (°C) and total annual precipitation (l/m^2)) from ACDC (2016) and biodiversity information. As biodiversity information we used total forest woody species richness (from NFI3) and forest bird richness (from Estrada et al., 2004) per municipality. Detailed information about these variables is provided in Appendix S1.

2.3. Data analysis

2.3.1. Data processing

ES supply needs to be referred to a given land surface to produce useful and comparable indicators. Some ES were expressed in % to land area and no further standardization was required (R4 and R5; Table 1). In all other cases, indicators were expressed in two ways, with the aim of reflecting two types of complementary information: (i) ES supply per unit of municipality area (referred here as land-based indicators); and (ii) supply per unit of forest cover (forest-based indicators). Forest-based indicators are in principle independent of the percentage of the municipalities' area covered by forests, which is likely to be an important driver of the spatial variation of land-based indicators.

Prior to analyze relationships among pairs of ES and with socio-environmental variables, ES values were transformed to make their statistical distribution closer to normality, by applying logarithmic or squared root functions when necessary (Table 1). In addition, proximity-to-target methodology was used to standardize their values to a common 0-1 scale (Rodríguez-Loinaz et al., 2015). In our case, lowest and highest benchmarks were determined from minimum (or maximum) values recorded for each ES and all intermediate values were rescaled linearly between the two extremes. After standardization, they were grouped and averaged for each municipality by category (provisioning, regulating and cultural), which involves giving equal weight to all indicators within a category (i.e., assuming that all indicators are relevant and similarly important).

2.3.2. Statistical analysis

Pearson correlations were used to explore the relationships (trade-offs and synergies; Mouchet et al., 2014) among normalized ES and their categories in space, as well as their relationships with socio-economic, climatic and biodiversity variables. The spatial aggregation of each ES was explored using Moran's I on a Spatial Autocorrelation Analysis (Moran, 1948; ESRI, 2013b). In addition, each normalized and standardized ES was modelled as a function of socioeconomic, climatic and biodiversity variables using linear mixed-effects models. To avoid multicollinearity issues, correlation and principal component analysis (PCA) were used to select a subgroup of independent variables to be included in the mixed-effects models as explanatory variables. As a result, we finally selected seven variables (population density, unemployment rate, population occupied in tertiary sector, mean annual temperature, total annual rainfall, woody species richness and bird richness) with correlation coefficients between them < 0.53. PCA confirmed that these variables were relatively orthogonal (Appendix 2, Fig. S2.1). County (groups of municipalities, N = 41, Fig. 1) was incorporated as a random factor to better account for spatial

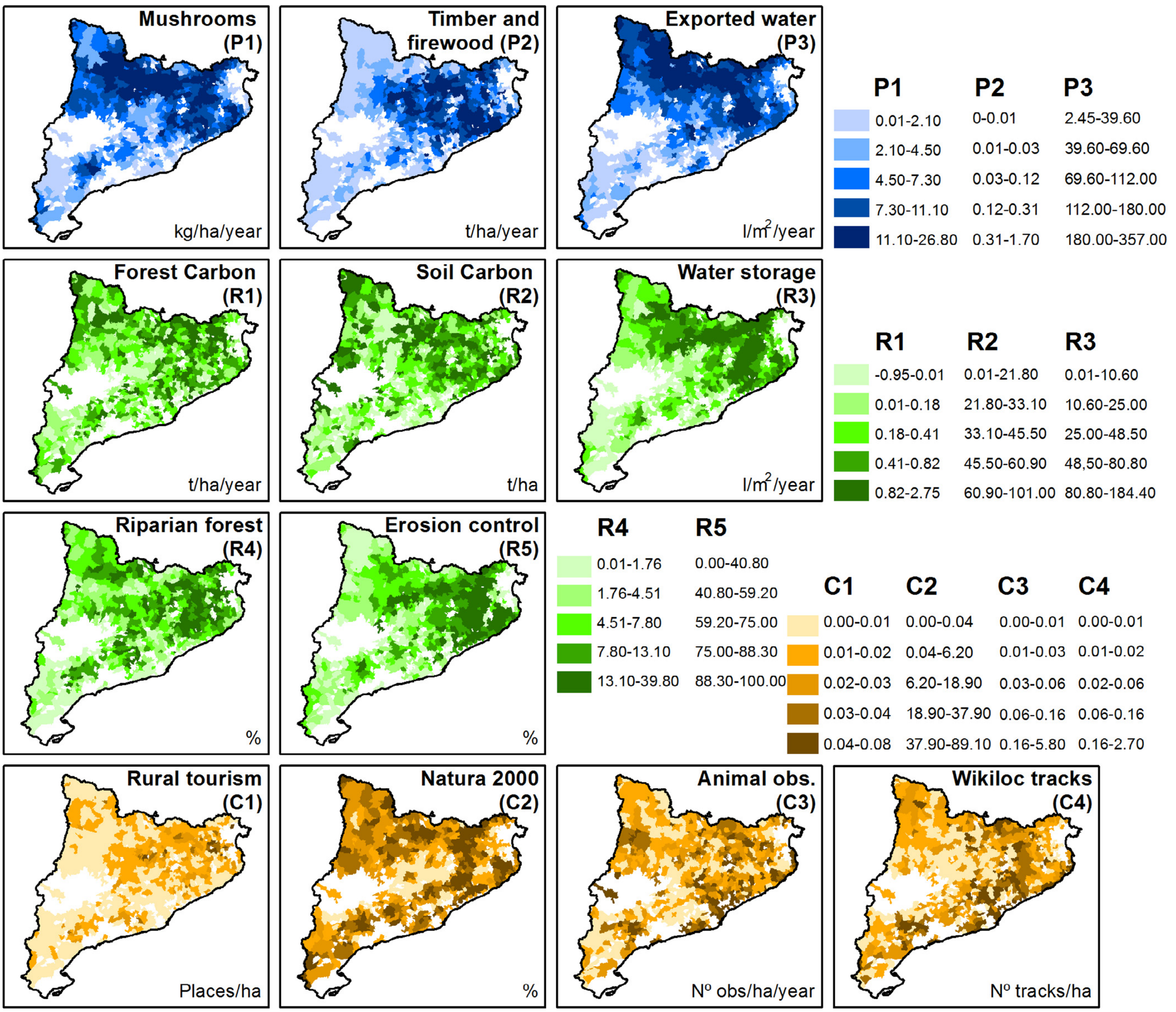

Fig. 2. Maps of all the ES land-based indicators, separated by ES category: provisioning (P), regulating (R) and cultural (C). In each plot municipalities are classified in five levels of supply (20% percentiles, see legends). White colour indicated no supply (non-forested municipalities).

autocorrelation. Preliminary analyses confirmed that including county as a random factor improved model fit (in terms of the Akaike Information Criterion, AIC). All statistical analyses were conducted using the R software environment (v.3.2.0; R Development Core Team, 2014). Finally in order to detect the areas with highest supply of the different categories of ES, a hotspot analysis on ES maps was performed (ESRI, 2013a) using the Getis-Ord Gi* clustering method (Getis and Ord, 1992; Schröter and Remme, 2016). A more detailed account of all these analyses is provided in the Supplementary Material (Appendix S2).

3. Results

3.1. Spatial distribution of ecosystem services

The spatial patterns of ES varied from highly clustered to dispersed, and many of them showed a gradient from mountainous areas (in the north) to lowlands (in the south) (Fig. 2 for land-based and Fig. 3 for forest-based indicators). Land-based indicators of food provision (P1) and water provision (P3) services showed a similar pattern with a concentration of high values in the North of the study area. High supply values for materials provision (P2) were concentrated in the Northeast. On the other hand, climate regulation and soil fertility (R1 and R2) had a rather scattered supply pattern. Other regulating services (R3, R4 and R5) were clustered in the eastern half and the Pyrenees mountains. Most cultural services (C2, C3 and C4) had complex patterns, with high-value supply areas being often close to the coast or the most populated zones. Highest values were observed in Eastern and particularly North-Eastern areas, close to the coast, including the pre-Pyrenees but also southern mountain ranges. The spatial patterns for forest-based indicators were generally similar to those of land-based indicators. However, some differences could be detected (compare Fig. 3 with Fig. 2). For instance, when forest-based indicators were used, high values of SOC-soil fertility (R2) and water regulation (R3) were more clustered in the Northwest, on mountainous municipalities.

Regarding the spatial aggregation of ES, provisioning and regulating services were more clustered (Moran's I index values between 0.36 and 0.54 for provisioning and 0.17–0.47 for regulating ES), whereas the spatial patterns of cultural services were more scattered throughout the study area (Moran's I = 0.06–0.25). All these values of Moran's I coefficient correspond to land-based indicators, but similar results were

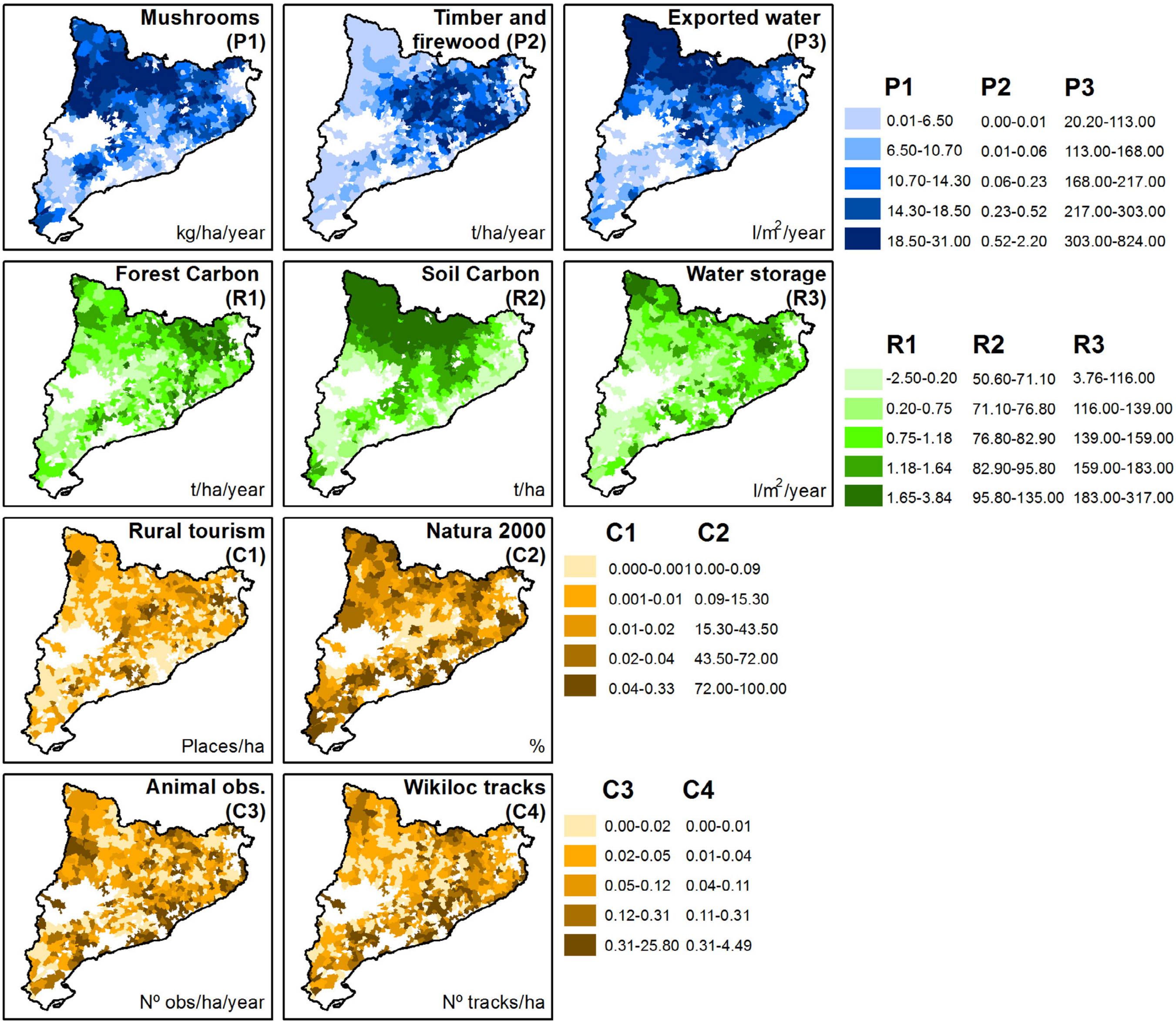

Fig. 3. Maps of all the ES forest-based indicators, separated by ES category: provisioning (P), regulating (R), and cultural (C). Indicators R4 and R5 are omitted because the distinction between land-based and forest-based indicators is not meaningful in their case. In each plot municipalities are classified in five levels of supply (20% percentiles, see legends). White colour indicated no supply (non-forested municipalities).

obtained when Moran's I was calculated for forest-based indicators (data not shown). Correlations between of the same ES expressed per unit land (land-based) and per unit forest (forest-based) were positive and highly significant in all cases (p-values < 0.001). These correlations were particularly high for provisioning ES ($r = 0.82$–0.99) and a little lower for cultural ($r = 0.62$–0.95) and regulating ES ($r = 0.25$–0.67).

When the overall distribution of the three categories of ES was compared (land-based indicators), two of them (provisioning and regulating) showed similar spatial patterns, with high supply areas clustered around the Pyrenees (particularly central and eastern areas; Fig. 4). Cultural ES were in general less clustered and their highest values occurred close to the Mediterranean coast. The hotspots distribution patterns for land-based indicators confirmed these patterns (Fig. 4) and showed that the highest supply areas for provisioning and regulating ES were clustered around the Eastern half of Pyrenees. Cultural ES had a more scattered distribution of hotspots throughout the study area. Hotspots for forest-based indicators are provided in the Supplementary materials (Fig. S3.1).

3.2. Relationships among ecosystem services and with socioeconomic, climatic and biodiversity variables

In general, land-based indicators showed positive pair-wise relationships (Table S3.1) while forest-based ones (Table S3.2) showed in some cases negative relationships, especially between cultural and other indicators. Positive associations were particularly strong among provisioning and regulating services, with highest values ($r > 0.7$) between water storage and mushroom production or water exported.

The comparison between ES categories showed highest correlations between provisioning and regulating ES for both land-based and forest-based indicators (Table 2). The correlation between these two ES categories and cultural ES was positive and significant for land-based indicators, but became non-significant when forest-based indicators were used. Regarding the relationships between categories of ES and climatic variables, temperature was negatively associated with provisioning, regulating and cultural ES (always significantly for land-based indicators). Rainfall was positively related to all ES categories when quantified using forest-based indicators. Biodiversity (woody species

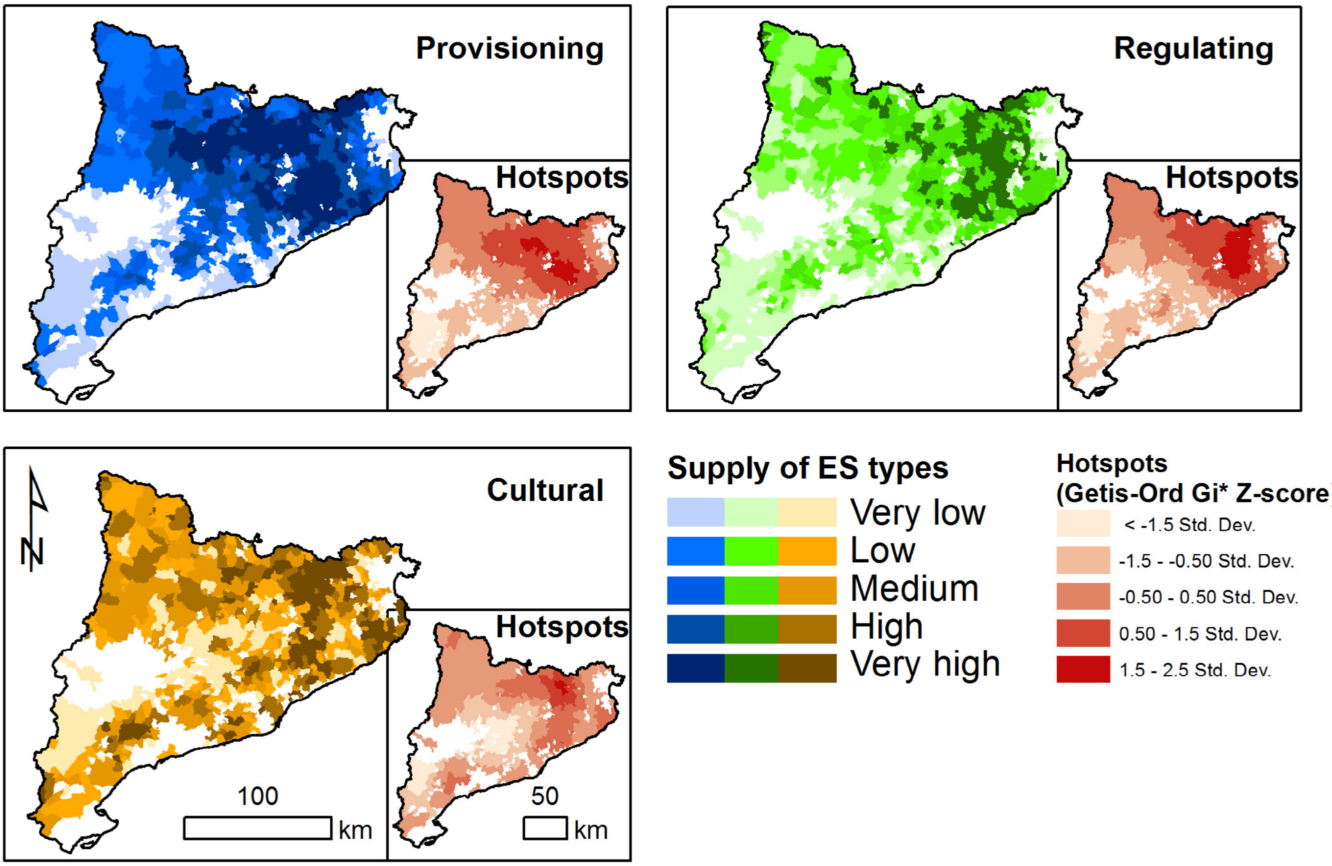

Fig. 4. Maps for the three categories of ES using land-based indicators, and location of their hotspot areas. The ES categories are classified in six levels of supply (a no-supply class and five 20% quantiles). Hotspots maps are classified in five categories using the standard deviation of Getis Ord Gi* statistic.

and bird richness) showed significant positive relationships with all services (land-based and forest-based, except for forest-based cultural services). Regarding socio-economic variables, the number of significant correlations with ES categories was lower. The percentage employment in agriculture was by far the variable showing more associations, showing negative relationships with the three categories of ES. Population density showed a negative relationship with regulating services (land-based) and a positive one with cultural ES (forest-based). Finally, the percentage of people employed in the tertiary sector showed positive associations with regulating and cultural services.

Linear mixed-effects models were used to explore the combined effects of socioeconomic, climatic and biodiversity drivers on the distribution of individual ES (see Table 3 for land-based indicators and Table S3.3 in Appendix S3 for forest-based ones). Explained variance ranged between 9 and 54% (marginal R^2) and between 13 and 79% (conditional R^2) for land-based indicators, being generally higher for provisioning ES. The range of explained variance was similar for forest-based indicators. Model results confirmed the dominant role of climatic variables in determining the spatial distribution of ES in the study area. Rainfall showed significant positive effects for 10 out of 12 land-based

Table 2
Correlations among ES categories and socio-environmental variables. Significant values (***P < 0.001 **0.01 *P < 0.05) are highlighted bold (positive relationships) and italic (negative relationships) characters.

Variables	Land-based type			Forest-based type		
	Prov.	Reg.	Cult.	Prov.	Reg.	Cult.
Provisioning	1.00	–	–	1.00	–	–
Regulating	**0.66*****	1.00	–	**0.50*****	1.00	–
Cultural	**0.31*****	**0.35*****	1.00	−0.07	0.03	1.00
Population dens.	−0.14	*−0.15**	0.01	−0.09	−0.11	**0.17****
Unemployment	−0.11	−0.08	0.00	−0.13	*−0.16***	0.11
Agriculture	*−0.15**	*−0.22****	*−0.24****	−0.11	*−0.18****	*−0.24****
Industry	0.13	0.10	−0.11	**0.15****	0.01	−0.10
Construction	0.01	0.06	0.07	−0.02	0.07	0.02
Tertiary sector	0.05	0.13	**0.28*****	0.02	**0.15***	**0.31*****
Temperature	*−0.31****	*−0.27****	*−0.18****	*−0.29****	*−0.55****	−0.02
Rainfall	**0.62*****	**0.56*****	**0.45*****	**0.54*****	**0.69*****	**0.18*****
Woody sp. richness	**0.46*****	**0.34*****	**0.26*****	**0.37*****	**0.29*****	0.10
Bird richness	**0.61*****	**0.47*****	**0.27*****	**0.59*****	**0.61*****	0.03

Table 3
Results of mixed-effects models performed for the 12 land-based indicators and some of the socio-environmental variables. Columns for each variable show the coefficient estimates plus/minus the standard error followed by their level of significance. $^{***}P < 0.001$ $^{**}0.01$ $^{*}P < 0.05$. R^2m: marginal R-squared. R^2c: conditional R-squared.

ES	Intercept	Population Density ($\times 10^{-5}$)	Unemployment ($\times 10^{-4}$)	Tertiary sector ($\times 10^{-4}$)	Mean Temperature ($\times 10^{-4}$)	Rainfall ($\times 10^{-4}$)	Woody sp. richness ($\times 10^{-4}$)	Bird richness ($\times 10^{-4}$)	R^2m	R^2c
Food provision (P1)	0.55 ± 0.65	−19.5 ± 4.2***	105.8 ± 53.0**	28.6 ± 28.7	−125.5 ± 29.9***	23.7 ± 3.9***	171.2 ± 21.1***	−77.6 ± 73.2	0.45	0.75
Materials provision (P2)	−11.22 ± 1.86***	−0.1 ± 1.1	−19.3 ± 158.4	−279.6 ± 85.7***	2575.0 ± 852.1***	4.3 ± 1.1***	407.8 ± 63.3***	299.4 ± 214.5	0.19	0.54
Water provision (P3)	2.59 ± 0.48***	−14.7 ± 3.1***	28.5 ± 39.3	16.4 ± 21.3	−671.7 ± 221.1***	23.7 ± 2.8***	89.3 ± 15.7***	55.9 ± 54.2	0.54	0.79
Climate regulation (R1)	−0.96 ± 0.32***	−1.5 ± 2.6	−8.6 ± 39.9	35.7 ± 20.2*	249.5 ± 142.2*	12.3 ± 1.9***	21.7 ± 16.1	−39.7 ± 45.5	0.16	0.18
Soil fertility (R2)	5.36 ± 1.32***	−25.9 ± 9.5***	44.2 ± 145.5	82.9 ± 76.2	−825.1 ± 596.4	31.9 ± 8.2***	29.9 ± 85.6	−292.1 ± 176.8*	0.13	0.21
Water regulation (R3)	−0.83 ± 0.81	−23.9 ± 0.5***	103.9 ± 69.4*	25.5 ± 37.6	193.9 ± 372.1	45.6 ± 4.9***	206.0 ± 27.7***	−165.5 ± 93.8*	0.45	0.69
Flood regulation (R4)	−3.91 ± 1.07***	−10.2 ± 6.9	−133.7 ± 101.5	2.4 ± 54.4	2112.0 ± 484.8***	2.5 ± 6.5	26.6 ± 40.7	833.8 ± 131.1***	0.16	0.36
Erosion control (R5)	2.47 ± 1.58	−3.4 ± 11.6	272.5 ± 177.5	−102.3 ± 92.6	533.2 ± 711.9	43.8 ± 9.8***	322.4 ± 75.9***	39.1 ± 213.7	0.18	0.25
Recreational (C1)	−0.06 ± 0.04	−0.8 ± 0.3***	−13.0 ± 4.2***	−3.4 ± 2.7	62.2 ± 19.7***	0.7 ± 0.3**	−2.5 ± 1.7	11.7 ± 5.5**	0.09	0.30
Existence (C2)	0.61 ± 1.96	−14.4 ± 13.5	289.9 ± 203.7	385.0 ± 107.9***	−2194.0 ± 890.2**	63.3 ± 12.2***	605.3 ± 81.9***	−1057.0 ± 254.1***	0.29	0.39
Experiential (C3)	−9.49 ± 1.21***	40.5 ± 8.2***	−42.7 ± 122.6	303.7 ± 65.3***	1931.0 ± 55.4***	3.8 ± 7.5	−152.6 ± 49.2***	488.8 ± 155.0***	0.18	0.33
Physical use (C4)	−0.43 ± 0.20**	4.6 ± 1.6***	21.2 ± 25.0	51.9 ± 12.7***	105.8 ± 90.6	2.8 ± 1.3**	0.6 ± 10.1	−20.8 ± 28.7	0.10	0.13

indicators (7 out of 10 for forest-based ones), while mean temperature was associated with 8 land-based (and 7 forest-based) ES, showing positive and negative relationships depending on the ES (Table 3 and Table S3.3). Woody species richness was the biodiversity variable with highest explanatory power. Its effect on land-based indicators was generally positive (significant in 7 cases), but it was significantly negative on animal observations. The number of negative effects for woody species richness was higher regarding forest-based indicators, including soil fertility, recreational and experiential. Bird richness showed less significant relationships and some of them were negative (i.e., existence-Natura 2000 for both types of indicators, soil fertility and water regulation for land-based ones, and climate regulation for forest-based ones). Finally, regarding socioeconomic variables, population density had a significant negative effect on 7 land-based indicators, although these relationships did not always remain significant when forest-based indicators were used. Population density was positively associated with two cultural ES (experiential and physical use), regardless of whether land-based or forest-based indices were used. Cultural ES indicators were positively related with the percentage population employed in the tertiary sector, except for recreational.

4. Discussion

4.1. Strengths and limitations of this study

In this work we combined models of ecological processes and different types of databases to produce a set of bio-physical indicators of a wide range of ES. Data sources were as close to underlying ecological processes as possible and included i) field sampling measures, ii) data from statistical models, iii) data from mechanistic models, iv) statistics from official administrative sources, v) information from cartographic sources and vi) data provided by associations for nature conservation and recreation. This set of ES indicators includes primary data and also accounts for structural properties of the ecosystems analyzed, which are often related with ES supply (Gamfeldt et al., 2013).

Most of the indicators used in this work (all except mushroom production, exported water and Natura 2000 network) represent the actual supply (or actual use *sensu* Schröter et al. (2014)) of the ES analyzed, and not their supply capacity (or capacity *sensu* Schröter et al. (2014)) (Table 1). This distinction is important for an accurate assessment of ES (Boerema et al., 2016). It should be noted that the relationship between actual supply and supply capacity differs among ES, reflecting differences in the context of ES delivery and the spatial configurations of supply capacity and demand (Burkhard et al., 2012; Schröter et al., 2014), which was not assessed in this study. In our case the selection of ES (measuring actual vs. supply capacity) primarily reflected limitations in data availability but also inherent differences between ES types (Yahdjian et al., 2015). In particular, the ES categories for which we mix indicators of actual and supply capacity (provisioning and cultural, Table 1) correspond to those for which the overlap between supply capacity and demand is relatively low (Yahdjian et al., 2015). In addition, we assumed that all our indicators of regulating ES represent actual supply, but this could be highly context-dependant (e.g. Andersson et al., 2014; Sutherland et al., 2017).

Selection of ES indicators is frequently problematic and our study is no exception. Firstly, we did not take into account some potentially important ES (particularly some cultural services such as traditional knowledge, hunting or educational aspects) because there was no information available at the level of analysis and for the type of ecosystems assessed. Secondly, some indicators that are used here to assess a specific ES could in fact be related with more than one ES. For instance, mushroom production is often associated with cultural values while we use it only as an indicator of food provision, and SOC can be also related with climate regulation, although its relationship with forest soil fertility is clearer (Chiti et al., 2012; Rodríguez-Loinaz et al., 2015). Our set of ES indicators represents a heterogeneous ensemble with large differences regarding their sources, calculation methods and spatial patterns. Approaches based on the application of a single, spatially explicit model to estimate forest ES are likely to be more robust and allow more flexibility in accounting for management or developing scenarios, but are normally limited to one or a few ES (e.g. Frank et al., 2015; Triviño et al., 2015; Vauhkonen and Ruotsalainen, 2017). On the other hand, combining data from different sources allows to cover a wider range of ES, potentially resulting in more complete assessments (i.e. Martínez-Harms and Balvanera, 2012; Martínez-Harms et al., 2016). In addition, the ES showed some differences between the temporal periods assessed. This limitation is not easy to avoid when heterogeneous data sources are used, and in our case we prioritized obtaining the best data available for the processes analysed in the study area, even at the cost of small temporal mismatches. Finally, some of the ES estimated here are based on previously tested (and published) ecological models (mushroom production, water exported, etc.), while others are based on simpler approaches using detailed LULC maps (riparian forest, erosion control or Natura 2000). Although we did not assess the accuracy or the uncertainty associated with these last data (Müller and Burkhard, 2012), they are based on best available information that provides an accurate representation of the studied landscape (LCMC, 2009).

Regarding the spatial level of analysis, although the municipality level is often used in ES assessments (e.g., Rodríguez-Loinaz et al., 2015), municipalities do not necessarily correspond to physical units in terms of environmental characteristics, forest distribution or forest function. Although more detailed, spatially explicit analyses are possible in some cases (e.g. erosion control in Guerra et al., 2016; catchment-level analyses for water-related ES in Stürck et al., 2014), this aggregation at municipality level has several advantages, as it allows: i) focusing the analysis on areas with a significant forest cover; ii) combining plot-level data (from NFI plots by calculation their average value) with other types of spatial information; iii) using administrative information that is not available (or meaningful) at more detailed spatial scales; and iv) an explicit link to the administrative level where most management strategies and land-use policies are decided and applied in general (Kroll et al., 2012; Ariza-Montobbio et al., 2014), and also in the study area. In addition, recent work in the same study area reports similar spatial patterns of ES at the municipality compared to finer (1×1 km) resolutions (Roces-Díaz et al., 2018).

4.2. Trade-offs and socioeconomic and environmental determinants of ES distribution

Land-based and forest-based indicators showed broadly similar spatial patterns, but important differences were detected in the analysis of trade-offs and synergies among ES using both approaches, which highlighted their complementary character. Positive and significant relations among ES categories were frequently obtained when using the land-based indicators but not always when using forest-based ones (Table 2). In addition, significant trade-offs between ES appeared only when forest-based indicators were compared (Table S3.2). Thus, referring ES to the total municipal area masked some of the relationships that were detected when they were expressed per unit of forest area. The selection of the type of indicator is likely context-dependent and, thus, deciding which one is more suitable based on first principles appears difficult. However, forest-based indicators better reflect the intrinsic properties of forests and therefore appear more appropriate when the aim of the study is to identify the fundamental trade-offs between different ES.

It is generally accepted that high biodiversity levels are associated to high levels of ES supply (Egoh et al., 2009; Gamfeldt et al., 2013). We used birds and woody species richness as biodiversity descriptors. Although this type of approach may be problematic because richness does not reflect changes in the abundance of species (Van Strien et al., 2012), there is no doubt that species richness is an important determinant of forest ecosystem function (e.g., Vila et al., 2007; Liang et al., 2016). Consistent with previous studies, our results showed positive correlations of provisioning and regulating services with woody species and bird richness (Table 3).

Climatic conditions (mean temperature and annual rainfall) were the main determinants of the spatial variation of the ES analyzed here (Tables 2 and 3 and Table S3.3), including the distribution of hotspots. That is a logical consequence of the relationships between ecological processes and climate, particularly in water-limited regions, but it could be also related with the fact that some of the ecological models used in this work (e.g., Doblas-Miranda et al., 2013; De Cáceres et al., 2015) use climatic conditions as drivers. For example, in the case of the soil water balance model, the exported water (P3) cannot be larger than rainfall

Cultural services often show a high demand from urban populations (Martín-López et al., 2012), which in the study area are closely associated to densely populated municipalities. Considering that all our cultural ES indicators measure ES use (actual supply), it is not surprising that two of them were positively related with population density (Table 3). In addition, animal observations showed clear positive relations with population density, in agreement with previous studies (Plieninger et al., 2013). The fact that three out of four ES showed positive relations with the percentage of people employed in the tertiary sector (Table 3) likely reflects the economic importance of tourism in the study area (Gary and Cànoves, 2011). Higher supply of cultural ES in forests surrounding urban areas could respond to the demand of these ES from people living in areas where contact with natural ecosystems is often limited (Daniel et al., 2012). Finally, negative relationships between provisioning services from agricultural agroecosystems and other ES are common (Haines-Young et al., 2011; Lee and Lautenbach, 2016), including those provided by forests (Rodríguez et al., 2007).

5. Conclusions

Our results provide a picture of the current supply of several ES by the forests of Catalonia. The integration of information from different sources allowed an assessment of these ES that overcomes some of the limitations and uncertainties derived from approaches based exclusively on land use/cover data. In addition, the calculation of all these ES at the municipal level allowed an analysis that can directly inform management. Although many ES showed highest values in the mountainous and wet areas of the North of the study area, the distribution patterns of some ES and biodiversity variables support a high ecological value of forest-dominated landscapes located close to the Mediterranean coast. The relevance of these landscapes in the Mediterranean Region has been highlighted in previous studies, both from the perspective of biodiversity (e.g., Fattorini et al., 2015) and using ES-based approaches (e.g., Brenner et al., 2010), and may require special attention in conservation strategies and ES management.

Additional research is required to assess possible changes in ES provision as a result of climate change in Mediterranean forested areas. Most of the ES indicators developed in this study allow for an explicit analysis of recent temporal trends (cf. Rodríguez-Loinaz et al., 2015) and can be included in structured forest dynamics models (e.g., de Cáceres et al., 2015). This information, together with the use of state-of-the-art ecological models should improve our capacity to forecast changes in the supply of ES under different climatic and socioeconomic scenarios.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecolind.2018.05.076.

References

ACDC, Atlas Climático de Cataluña. Departament de Geografía. Unitat de Botánica. Universidad Autónoma de Barcelona. Consulta on-line (05/05/2016). http://www.opengis.uab.cat/acdc/en_index.htm.

Alamgir, M., Turton, S.M., Macgregor, C.J., Pert, P.L., 2016. Ecosystem services capacity across heterogeneous forest types: understanding the interactions and suggesting pathways for sustaining multiple ecosystem services. Sci. Total Environ. 566, 584–595. http://dx.doi.org/10.1016/j.scitotenv.2016.05.107.

Andersson, E., McPhearson, T., Kremer, P., Gomez-Baggethun, E., Haase, D., Tuvendal, M., Wurster, D., 2014. Scale and context dependence of ecosystem service providing units. Ecosyst. Serv. 15, 157–164. http://dx.doi.org/10.1016/j.ecoser.2014.08.001.

Andrew, M.E., Wulder, M.A., Nelson, T.A., Coops, N.C., 2015. Spatial data, analysis approaches, and information needs for spatial ecosystem service assessments: a review. GIScience Remote Sens. 52, 344–373. http://dx.doi.org/10.1080/15481603.2015.1033809.

Ariza-Montobbio, P., Farrell, K.N., Gamboa, G., Ramos-Martin, J., 2014. Integrating energy and land-use planning: socio-metabolic profiles along the rural – urban continuum in Catalonia (Spain). Environ. Dev. Sustain. 16, 925–956. http://dx.doi.org/10.1007/s10668-014-9533-x.

Boerema, A., Rebelo, A.J., Bodi, M.B., Esler, K.J., Meire, P., 2016. Are ecosystem services adequately quantified? J. Appl. Ecol. 54, 358–370. http://dx.doi.org/10.1111/1365-2664.12696.

Bonet, J.A., Palahí, M., Colinas, C., Pukkala, T., Fischer, C.R., Miina, J., Martínez de Aragón, J., 2010. Modelling the production and species richness of wild mushrooms in pine forests of the Central Pyrenees in northeastern Spain. Can. J. For. Res. 40, 347–356. http://dx.doi.org/10.1139/X09-198.

Brenner, J., Jiménez, J.A., Sardá, R., Garola, A., 2010. An assessment of the non-market value of the ecosystem services provided by the Catalan coastal zone, Spain. Ocean Coast. Manage. 53, 27–38. http://dx.doi.org/10.1016/j.ocecoaman.2009.10.008.

Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D., Rodrigues, A.S.L., 2006. Global biodiversity conservation priorities. Science 313, 58–61. http://dx.doi.org/10.1126/science.1127609.

Bugalho, M.N., Caldeira, M.C., Pereira, J.S., Aronson, J., Pausas, J.G., 2011. Mediterranean cork oak savannas require human use to sustain biodiversity and ecosystem services. Front. Ecol. Environ. 9, 278–286. http://dx.doi.org/10.1890/100084.

Burkhard, B., Kroll, F., Nedkov, S., Müller, F., 2012. Mapping ecosystem service supply, demand and budgets. Ecol. Indic. 21, 17–29. http://dx.doi.org/10.1016/j.ecolind.2011.06.019.

Chiti, T., Díaz-Pinés, E., Rubio, A., 2012. Soil organic carbon stocks of conifers, broadleaf and evergreen broadleaf forests of Spain. Biol. Fertil. Soils 48, 817–826. http://dx.doi.org/10.1007/s00374-012-0676-3.

Costanza, R., Arge, R., Groot, R. De, Farberk, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., Neill, R.V.O., Paruelo, J., Raskin, R.G., Suttonkk, P., 1997. The value of the world' s ecosystem services and natural capital. Nature 387, 253–260.

Daniel, T.C., Muhar, A., Arnberger, A., Aznar, O., Boyd, J.W., Chan, K.M., Costanza, R., Elmqvist, T., Flint, C.G., Gobster, P.H., Gret-Regamey, A., Lave, R., Muhar, S., Penker, M., Ribe, R.G., Schauppenlehner, T., Sikor, T., Soloviy, I., Spierenburg, M., Taczanowska, K., Tam, J., von der Dunk, A., 2012. Contributions of cultural services to the ecosystem services agenda. Proc. Natl. Acad. Sci. 109, 8812–8819. http://dx.doi.org/10.1073/pnas.1114773109.

De Cáceres, M., Martínez-Vilalta, J., Coll, L., Llorens, P., Casals, P., Poyatos, R., Brotons, L., 2015. Coupling a water balance model with forest inventory data to predict drought stress: the role of forest structural changes vs. climate changes. Agric. Forest Meteorol. 213, 77–90. http://dx.doi.org/10.1016/j.agrformet.2015.06.012.

de-Miguel, S., Bonet, J.A., Pukkala, T., Martínez de Aragón, J., 2014. Impact of forest management intensity on landscape-level mushroom productivity: a regional model-based scenario analysis. For. Ecol. Manage. 330, 218–227. http://dx.doi.org/10.1016/j.foreco.2014.07.014.

Doblas-Miranda, E., Martinez-Vilalta, J., Lloret, F., Alvarez, A., Avila, A., Bonet, F.J., Brotons, L., Castro, J., Curiel Yuste, J., Diaz, M., Ferrandis, P., Garcia-Hurtado, E., Iriondo, J.M., Keenan, T.F., Latron, J., Llusia, J., Loepfe, L., Mayol, M., More, G., Moya, D., Peñuelas, J., Pons, X., Poyatos, R., Sardans, J., Sus, O., Vallejo, V.R., Vayreda, J., Retana, J., 2015. Reassessing global change research priorities in mediterranean terrestrial ecosystems: how far have we come and where do we go from here? Glob. Ecol. Biogeogr. 24, 25–43. http://dx.doi.org/10.1111/geb.12224.

Doblas-Miranda, E., Rovira, P., Brotons, L., Martínez-Vilalta, J., Retana, J., Pla, M., Vayreda, J., 2013. Soil carbon stocks and their variability across the forests, shrublands and grasslands of peninsular Spain. Biogeosciences 10 (12), 8353–8361. http://dx.doi.org/10.5194/bg-10-8353-2013.

Duncker, P.S., Raulund-rasmussen, K., Gundersen, P., Katzensteiner, K., Jong, J. De, Peter, H., 2012. How forest management affects ecosystem services, including timber production and economic return: synergies and trade-offs. Ecol. Soc. 17 (40), 50. http://dx.doi.org/10.5751/ES-05066-170450.

Egoh, B., Reyers, B., Rouget, M., Bode, M., Richardson, D., 2009. Spatial congruence between biodiversity and ecosystem services in South Africa. Biol. Conserv. 142, 553–562. http://dx.doi.org/10.1016/j.biocon.2008.11.009.

Eigenbrod, F., Armsworth, P.R., Anderson, B.J., Heinemeyer, A., Gillings, S., Roy, D.B., Thomas, C.D., Gaston, K.J., 2010. The impact of proxy-based methods on mapping the distribution of ecosystem services. J. Appl. Ecol. 47, 377–385. http://dx.doi.org/10.1111/j.1365-2664.2010.01777.x.

EME, 2011. Evaluación de los Ecosistemas del Milenio en España, Ecosistemas y Biodiversidad para el Bienestar Humano, Evaluación de los Ecosistemas del Milenio en España, Síntesis de resultados. Fundación Biodiversidad. Ministerio de Medio Ambiente, y Medio Rural y Marino.

ESRI, 2013a. How Hot Spot Analysis (Getis-Ord Gi*) works, ARCGIS Resources, ArcGIS 10 Help. [online 15 July 2015] URL: http://resources.arcgis.com/en/help/main/10.1/index.html#/How_Hot_Spot_Analysis_Getis_Ord_Gi_works/005p00000011000000/.

ESRI, 2013b. How Spatial Autocorrelation (Global Moran's I) works. [online] URL: http://resources.arcgis.com/en/help/main/10.1/index.html#//005p0000000t000000.

Estrada, J., Pedrocchi, V., Brotons, L., Herrando, S., (Eds). 2004. Atles dels Ocells Nidificants de Catalunya 1999-2002. Institut Català d'Ornitologia (ICO)/Lynx Edicions, Barcelona.

FAO, Food and Agriculture Organization of the United Nations. 2014. State of the Worlds Forests: Enhancing the socioeconomic benefits from forests. Rome. ISSN 1020-5705. 119 pp.

Fattorini, S., Maltzeff, P., Salvati, L., 2015. Use of insect distribution across landscape-soil units to assess conservation priorities in a Mediterranean coastal reserve: the tenebrionid beetles of Castelporziano (Central Italy). Rend. Lincei 26, 353–366. http://dx.doi.org/10.1007/s12210-015-0391-8.

Frank, S., Fürst, C., Pietzsch, F., 2015. Cross-sectoral resource management: how forest management alternatives affect the provision of biomass and other ecosystem services. Forests 6, 533–560. http://dx.doi.org/10.3390/f6030533.

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Fröberg, M., Stendahl, J., Philipson, C.D., Mikusiński, G., Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J., Bengtsson, J., 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. Nat. Commun. 4, 1340. http://dx.doi.org/10.1038/ncomms2328.

Garcia-Llorente, M., Iniesta-arandia, I., Willaarts, B.A., Harrison, P.A., Berry, P., del Bayo, M., Castro, A.J., Montes, C., Martín-López, B., 2015. Biophysical and sociocultural factors underlying spatial trade-offs of ecosystem services in semiarid watersheds. Ecol. Soc. 20, 39. http://dx.doi.org/10.5751/ES-07785-200339.

García-Nieto, A.P., García-Llorente, M., Iniesta-Arandia, I., Martín-López, B., 2013. Mapping forest ecosystem services: From providing units to beneficiaries. Ecosyst. Serv. 4, 126–138. http://dx.doi.org/10.1016/j.ecoser.2013.03.003.

Gary, L., Cànoves, G., 2011. Life cycles, stages and tourism history. The Catalonia (Spain) experience. Ann. Tourism Res. 38, 651–671.

Generalitat de Catalunya, 2014. Statistics of public and private forest harvest. Unpublished data.

Generalitat de Catalunya, 2015. Xarxa Natura 2000. Departament de Territori i Sostenibilitat. Consulta on-line (05/05/2016). http://mediambient.gencat.cat/ca/05_ambits_dactuacio/patrimoni_natural/senp_catalunya/el_sistema/xarxa_natura_2000.

Getis, A., Ord, J.K., 1992. The analysis of spatial association. Geogr. Anal. 24, 189–206. http://dx.doi.org/10.1111/j.1538-4632.1992.tb00261.x.

Grove, T., Rackham, O., 2003. The Nature of Mediterranean Europe. An Ecological History. Yale University Press, New Haven.

Guerra, C.A., Maes, J., Geijzendorffer, I., Metzger, M.J., 2016. An assessment of soil erosion prevention by vegetation in Mediterranean Europe: current trends of ecosystem service provision. Ecol. Indic. 60, 213–222. http://dx.doi.org/10.1016/j.ecolind.2015.06.043.

Haines-Young, R., Potschin, M., 2013. Towards a common International Classification of Ecosystem Services (CICES): Version 4.3 [online 15 July 2015] URL: www.cices.eu/.

Haines-Young, R., Potschin, M., Kienast, F., 2011. Indicators of ecosystem service potential at European scales: mapping marginal changes and trade-offs. Ecol. Indic. http://dx.doi.org/10.1016/j.ecolind.2011.09.004.

Hampe, A., Petit, R.J., 2005. Conserving biodiversity under climate change: the rear edge matters. Ecol. Lett. 8, 461–467. http://dx.doi.org/10.1111/j.1461-0248.2005.00739.x.

Hein, L., van Koppen, K., de Groot, R.S., van Ierland, E.C., 2006. Spatial scales, stakeholders and the valuation of ecosystem services. Ecol. Econ. 57, 209–228. http://dx.doi.org/10.1016/j.ecolecon.2005.04.005.

Hou, Y., Burkhard, B., Müller, F., 2013. Uncertainties in landscape analysis and ecosystem service assessment. J. Environ. Manage. http://dx.doi.org/10.1016/j.jenvman.2012.12.002.

IDESCAT, Institut ́dEstadística de Catalunya. 2015. Información demográfica y económica por municipios. Consulta on-line. http://www.idescat.cat/es/.

Kroll, F., Muller, F., Haase, D., Fohrer, N., 2012. Rural-urban gradient analysis of ecosystem services supply and demand dynamics. Land Use Policy 29, 521–535. http://dx.doi.org/10.1016/j.landusepol.2011.07.008.

LCMC, Land Cover Map of Catalonia, 2009. Generalitat de Catalunya. CREAF, Universidad Autónoma de Barcelona. http://www.creaf.uab.es/mcsc/esp/index.htm.

Lee, H., Lautenbach, S., 2016. A quantitative review of relationships between ecosystem services. Ecol. Indic. 66, 340–351. http://dx.doi.org/10.1016/j.ecolind.2016.02.004.

Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.-D., McGuire, D., Bozzato, F., Pretzsch, H., De-Miguel, S., Paquette, A., Hérault, B., Scherer-Lorenzen, M., Barrett, C.B., Glick, H.B., Hengeveld, G.M., Nabuurs, G.-J., Pfautsch, S., Viana, H., Vibrans, A.C., Ammer, C., Schall, P., Verbyla, D., Tchebakova, N., Fischer, M., Watson, J.V., Chen, H.Y.H., Lei, X., Schelhaas, M.-J., Lu, H., Gianelle, D., Parfenova, E.I., Salas, C., Lee, E., Lee, B., Kim, H.S., Bruelheide, H., Coomes, D.A., Piotto, D., Sunderland, T., Schmid, B., Gourlet-Fleury, S., Sonké, B., Tavani, R., Zhu, J., Brandl, S., Vayreda, J., Kitahara, F., Searle, E.B., Neldner, V.J., Ngugi, M.R., Baraloto, C., Frizzera, L., Balazy, R., Oleksyn, J., Zawila-Niedzwiecki, T., Bouriaud, O., Bussotti, F., Finér, L., Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski, A.M., Peri, P.L., Gonmadje, C., Marthy, W., O'Brien, T., Martin, E.H., Marshall, A., Rovero, F., Bitariho, R., Niklaus, P.A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F., Wortel, V., Engone-Obiang, N.L., Ferreira, L.V., Odeke, D.E., Vasquez, R.M., Reich, P.B., 2016. Positive biodiversity–productivity relationship predominant in global forests. Science (80-.) 354, 196–208. http://dx.doi.org/10.1126/science.aaf8957.

MAGRAMA, Ministerio de Agricultura, Alimentación y Medio Ambiente. 1997–2007. Segundo y Tercer Inventario Forestal Nacional. Gobierno de España. [online 15 July 2015] URL: http://www.magrama.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/index_inventario_forestal.aspx.

Martínez-Harms, M.J., Balvanera, P., 2012. Methods for mapping ecosystem service supply: a review. Int. J. Biodivers. Sci. Ecosyst. Serv. Manage. 8, 17–25. http://dx.doi.org/10.1080/21513732.2012.663792.

Martínez-Harms, M.J., Quijas, S., Merenlender, A.M., Balvanera, P., 2016. Enhancing ecosystem services maps combining field and environmental data. Ecosyst. Serv. 22, 32–40. http://dx.doi.org/10.1016/j.ecoser.2016.09.007.

Martínez-Vilalta, J., Piñol, J., 2002. Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. For. Ecol. Manage. 161, 247–256. http://dx.doi.org/10.1016/S0378-1127(01)00495-9.

Martín-López, B., Iniesta-Arandia, I., García-Llorente, M., Palomo, I., Casado-Arzuaga, I., Del Amo, D.G., Gómez-Baggethun, E., Oteros-Rozas, E., Palacios-Agundez, I., Willaarts, B., González, J.A., Santos-Martín, F., Onaindia, M., López-Santiago, C., Montes, C., 2012. Uncovering ecosystem service bundles through social preferences. PLoS One 7. http://dx.doi.org/10.1371/journal.pone.0038970.

MEA, 2005. Ecosystems and Human Well-being: Current State and Trends. Island Press, Washington, DC Millennium Ecosystem Assessment.

Medail, F., Quezel, P., 1999. Biodiversity hotspots in the Mediterranean Basin: setting global conservation priorities. Conserv. Biol. 13, 1510–1513. http://dx.doi.org/10.1046/j.1523-1739.1999.98467.x.

Miura, S., Amacher, M., Hofer, T., San-Miguel-Ayanz, J., Ernawati, Thackway, R., 2015. Protective functions and ecosystem services of global forests in the past quarter-century. For. Ecol. Manage. 352, 35–46. http://dx.doi.org/10.1016/j.foreco.2015.03.039.

Moran, P.A.P., 1948. The interpretation of statistical maps. J. R. Stat. Soc. 10, 243–251.

Mouchet, M., Lamarque, P., Martín-López, B., Crouzat, E., Gos, P., Byczek, C., Lavorel, S., 2014. An interdisciplinary methodological guide for quantifying associations between ecosystem services. Glob. Environ. Change 28, 298–308. http://dx.doi.org/10.1016/j.gloenvcha.2014.07.012.

Müller, F., Burkhard, B., 2012. The indicator side of ecosystem services. Ecosyst. Serv. 1, 26–30. http://dx.doi.org/10.1016/j.ecoser.2012.06.001.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. http://dx.doi.org/10.1038/35002501.

Peñuelas, J., Boada, M., 2003. A global change-induced biome shift in the Montseny mountains (NE Spain). Glob. Chang. Biol. 9, 131–140. http://dx.doi.org/10.1046/j.1365-2486.2003.00566.x.

Plieninger, T., Dijks, S., Oteros-Rozas, E., Bieling, C., 2013. Assessing, mapping, and quantifying cultural ecosystem services at community level. Land Use Policy 33, 118–129. http://dx.doi.org/10.1016/j.landusepol.2012.12.013.

Plummer, M.L., 2009. Assessing benefit transfer for the valuation of ecosystem services. Front. Ecol. Environ. 7, 38–45. http://dx.doi.org/10.1890/080091.

Quintas-Soriano, C., Castro, A.J., García-Llorente, M., Cabello, J., Castro, H., 2014. From supply to social demand: a landscape-scale analysis of the water regulation service. Landsc. Ecol. 29, 1069–1082. http://dx.doi.org/10.1007/s10980-014-0032-0.

R Development Core Team. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing; 2014. Retrieved April 10, 2014, from www.r-project.org/.

Roces-Díaz, J.V., Burkhard, B., Kruse, M., Muller, F., Álvarez-Álvarez, P., Diaz-Varela, E., 2017. Use of ecosystem information derived from forest thematic maps for spatial analysis of ecosystem services in northwestern Spain. Lands. Ecol. Eng. 13, 45–57. http://dx.doi.org/10.1007/s11355-016-0298-2.

Roces-Díaz, J.V., Vayreda, J., Banqué-Casanovas, M., Díaz-Varela, E., Bonet, J.A., Brotons, L., de-Miguel, S., Herrando, S., Martínez-Vilalta, J., 2018. The spatial level of analysis affects the patterns of forest ecosystem services supply and their relationships. Sci. Total Environ. 626, 1270–1283. http://dx.doi.org/10.1016/j.scitotenv.2018.01.150.

Rodríguez, J.P., Beard, T.D., Bennett, E.M., Cumming, G.S., Cork, S.J., Agard, J., Dobson, A.P., Peterson, G.D., 2007. Trade-offs across space, time, and ecosystem services. Ecol. Soc. 11, 28. URL: http://www.ecologyandsociety.org/vol11/iss1/art28/.

Rodríguez-Loinaz, G., Alday, J.G., Onaindia, M., 2015. Multiple ecosystem services landscape index: a tool for multifunctional landscapes conservation. J. Environ. Manage. 147, 152–163. http://dx.doi.org/10.1016/j.jenvman.2014.09.001.

Ruiz-Benito, P., Gomez-Aparicio, L., Paquette, A., Messier, C., Kattge, J., Zavala, M.A., 2014. Diversity increases carbon storage and tree productivity in Spanish forests. Glob. Ecol. Biogeogr. 23, 311–322. http://dx.doi.org/10.1111/geb.12126.

Schröter, M., Barton, D.N., Remme, R.P., Hein, L., 2014. Accounting for capacity and flow of ecosystem services: a conceptual model and a case study for Telemark. Norway. Ecol. Indic. 36, 539–551. http://dx.doi.org/10.1016/j.ecolind.2013.09.018.

Schröter, M., Remme, R.P., 2016. Spatial prioritisation for conserving ecosystem services: comparing hotspots with heuristic optimisation. Landsc. Ecol. 31, 431–450. http://dx.doi.org/10.1007/s10980-015-0258-5.

Sutherland, I.J., Gergel, S.E., Bennett, E.M., 2016. Seeing the forest for its multiple ecosystem services: indicators for cultural services in heterogeneous forests. Ecol. Indic. 71, 123–133. http://dx.doi.org/10.1016/j.ecolind.2016.06.037.

Sutherland, I.J., Villamagna, A.M., Dallaire, C.O., Bennett, E.M., Chin, A.T., Yeung, A.C., Lamothe, K.A., Tomscha, S.A., Cormier, R., 2017. Undervalued and under pressure: a plea for greater attention toward regulating ecosystem services. Ecol. Indic. http://dx.doi.org/10.1016/j.ecolind.2017.06.047.

Stürck, J., Poortinga, A., Verburg, P.H., 2014. Mapping ecosystem services: the supply and demand of flood regulation services in Europe. Ecol. Indic. 38, 198–211. http://dx.doi.org/10.1016/j.ecolind.2013.11.010.

Thom, D., Seidl, R., 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. Biol. Rev. 91, 760–781. http://dx.doi.org/10.1111/brv.12193.

Triviño, M., Juutinen, A., Mazziotta, A., Miettinen, K., Podkopaev, D., Reunanen, P., Mönkkönen, M., 2015. Managing a boreal forest landscape for providing timber, storing and sequestering carbon. Ecosyst. Serv. 14, 179–189. http://dx.doi.org/10.1016/j.ecoser.2015.02.003.

Trumbore, S., Brando, P., Hartmann, H., 2015. Forest health and global change. Science. 349, 814–818. http://dx.doi.org/10.1126/science.aac6759.

Underwood, E.C., Viers, J.H., Klausmeyer, K.R., Cox, R.L., Shaw, M.R., 2009. Threats and biodiversity in the mediterranean biome. Divers. Distrib. 15, 188–197. http://dx.doi.org/10.1111/j.1472-4642.2008.00518.x.

Van der Biest, K., Vrebos, D., Staes, J., Boerema, A., Bodi, M.B., Fransen, E., Meire, P., 2015. Evaluation of the accuracy of land-use based ecosystem service assessments for different thematic resolutions. J. Environ. Manage. 156, 41–51. http://dx.doi.org/10.1016/j.jenvman.2015.03.018.

Van Strien, A.J., Soldaat, L.L., Gregory, R.D., 2012. Desirable mathematical properties of indicators for biodiversity change. Ecol. Indic. 14, 202–208. http://dx.doi.org/10.1016/j.ecolind.2011.07.007.

Vauhkonen, J., Ruotsalainen, R., 2017. Assessing the provisioning potential of ecosystem services in a Scandinavian boreal forest: suitability and tradeoff analyses on grid-based wall-to-wall forest inventory data. For. Ecol. Manage. 389, 272–284. http://dx.doi.org/10.1016/j.foreco.2016.12.005.

Vayreda, J., Martinez-Vilalta, J., Gracia, M., Retana, J., 2012. Recent climate changes interact with stand structure and management to determine changes in tree carbon stocks in Spanish forests. Glob. Chang. Biol. 18, 1028–1041. http://dx.doi.org/10.1111/j.1365-2486.2011.02606.x.

Vila, M., Basnou, C., Pysek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A., Roy, D., Hulme, P.E., 2010. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Front. Ecol. Environ. 8, 135–144. http://dx.doi.org/10.1890/080083.

Vila, M., Vayreda, J., Comas, L., Ibañez, J.J., Mata, T., Obon, B., 2007. Species richness and wood production: A positive association in Mediterranean forests. Ecol. Lett. 10, 241–250. http://dx.doi.org/10.1111/j.1461-0248.2007.01016.x.

Yahdjian, L., Sala, O.E., Havstad, K.M., 2015. Rangeland ecosystem services: shifting focus from supply to reconciling supply and demand. Front. Ecol. Environ. 13, 44–51. http://dx.doi.org/10.1890/140156.