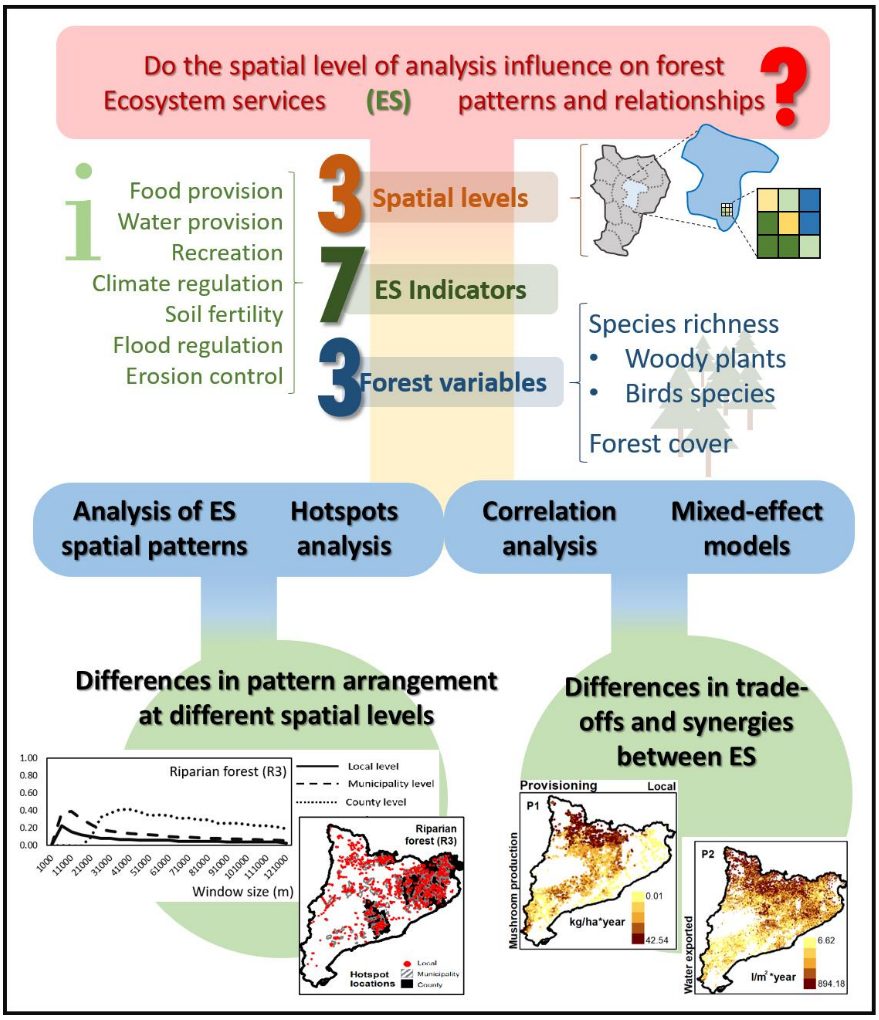
The spatial level of analysis affects the patterns of forest ecosystem services supply and their relationships

Highlights

- Scale is a relevant aspect in the analysis and of Ecosystem Services (ES)
- The effects of the spatial level of analysis on 7 ES indicators were assessed
- ES Indicators were estimated at local ($1km^2$), municipality and county levels
- Averaging effects at higher spatial levels obscured local ES heterogeneity patterns
- Identification of hotspots and ES relationships depend on the level of analysis



The spatial level of analysis affects the patterns of forest ecosystem services supply and their relationships

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Abstract

The implementation of the Ecosystem Services (ES) framework (including supply and demand) should be based on accurate spatial assessments to make it useful for land planning or environmental management. Despite the inherent dependence of ES assessments on the spatial resolution at which they are conducted, the studies analysing these effects on ES supply and their relationships are still scarce. To study the influence of the spatial level of analysis on ES patterns and on the relationships among different ES, we selected seven indicators representing ES supply and three variables that describe forest cover and biodiversity for Catalonia (NE Iberian Peninsula). These indicators were estimated at three different scales: local, municipality and county. Our results showed differences in the ES patterns among the levels of analysis. The higher levels (municipality/county) removed part of the local heterogeneity of the patterns observed at the local scale, particularly for ES indicators characterized by a finely grained, scattered distribution. The relationships between ES indicators were generally similar at the three levels. However, some negative relationships (potential trade-offs) that were detected at the local level changed to positive (and significant) relationships at municipality and county. Spatial autocorrelation showed similarities between patterns at local and municipality levels, but differences with county level. We conclude that the use of high-resolution spatial data is preferable whenever available, in particular when identifying hotspots or trade-offs/synergies is of primary interest. When the main objective is describing broad patterns of ES, intermediate levels (e.g., municipality) are also adequate, as they conserve many of the properties of assessments conducted at finer scales, allowing the integration of data sources and, usually, being more directly relevant for policy-making. In conclusion, our results warn against the uncritical use of coarse (aggregated) spatial ES data and indicators in strategies for land use planning and forest conservation.

Keywords

Indicators; forest biodiversity; administrative boundaries; scale effects; trade-off and synergy; upscaling

1. Introduction

Ecosystem services (ES) can be defined as those benefits provided directly and indirectly by the ecological functioning of nature, and they are key for the wellbeing of human societies (MEA, 2005). This concept bridges science-based and societal considerations and has been growing in relevance since the 1990s. Thus, different international initiatives appeared in the last 20 years focused on their assessment (i.e. MEA, 2005; TEEB, 2010; IPBES, 2012), together with a growing scientific interest (Seppelt et al., 2011; Boerema et al., 2016). Different authors have highlighted the potential applications of the ES concept for sustainable land use planning (Daily et al., 2009; Baró et al., 2016), natural resources management (Tallis and Polasky, 2009) or biodiversity conservation (Chan et al., 2011). At the same time, there is a need to develop integrative frameworks for ES assessment (Kremen, 2005; de Groot et al., 2010) including biodiversity, bio-physical and social aspects of the environment, and also covering as much as possible the different components of ES (cascade approach including supply, demand and flow) (Potschin and Haines-Young, 2010; Yahdjian et al., 2015).

The implementation of environmental management based on ES needs to be based on spatial approaches (Egoh et al., 2008; Andrew et al., 2015) that involve mapping and characterizing both ES supply and demand (Burkhard et al., 2012). Consistent with this, most ES assessments (and ES-based studies) performed in recent years have included a spatially explicit perspective (Seppelt et al., 2011). However, different authors have pointed out the need to account for spatial patterns in more rigorous ways (Boerema et al., 2016) and to reduce the uncertainty associated with ES mapping methods (Hou et al., 2013). The effect of scale on ES distribution patterns and their spatial relationships has been highlighted in different works (e.g., Martín-López et al., 2009; Geijzendorffer et al., 2015). As ES are generated by different ecosystem types and ecological processes with different spatial patterns, their supply may differ between scales (Hein et al., 2006; Roces-Díaz et al., 2014). Although the analysis of spatial patterns at landscape and regional scales is extensively developed through spatial statistics, landscape metrics and spatially explicit models (e.g. Wagner and Fortin, 2005; Uuemaa et al., 2009; Fortin et al., 2012; Uuemaa et al., 2013), there is a limited knowledge on what are the most appropriate scales of analysis to assess ES and their spatial relationships for different applications in the context of land management, policy and decision making (Andrew et al., 2015; Schröter et al., 2015).

Importantly, scale effects cannot only affect the absolute values of ES indicators but also the relationships among them (Xu et al., 2017). When the provision of a given ES is increased at the expense of another ES a trade-off occurs, while a mutual positive relationship, in which both ES increase at the same time, can be defined as a synergy (Rodriguez et al., 2006; Bennett et al., 2009). Previous work did not find large differences on the relationships between ES patterns and biodiversity comparing different pixel sizes (Anderson et al., 2009), and similar ES patterns across different administrative levels and spatial scales has been reported (Raudssep-Hearne and Peterson, 2016). It is unknown, however, whether these results can be generalized.

For ES assessments to be useful for planning and management objectives they need to be conducted at relevant spatial scales, which frequently correspond to administrative levels, as those facilitate policy implementation (Tolvanen et al., 2014). The UN Strategic Plan for

Biodiversity 2011-2020 urges subnational administrations to consider the development of biodiversity strategies to achieve the targets on biodiversity conservation, including the provision of ES (Aichi goal D, CBD, 2011-2020). In this way the role of regional (Schulp et al., 2014), county (Chen et al., 2009) and municipality (Rodriguez-Loinaz et al., 2015; Renard et al., 2015) administrations is becoming more relevant to assess ES and the corresponding policy-making at these subnational levels. At the same time, increasing the spatial level of analysis is at the cost of homogenization of landscape patterns and loss of local information (Díaz-Varela et al., 2009; 2016).

In this work we explored the effects of using different spatial levels of analysis on ES patterns and their spatial relationships, in order to improve the integration of the ES framework on national and sub-national strategies for planning and conservation of natural resources. The specific objectives of this work are to: i) analyse the effects of spatial resolution on the spatial patterns of forest ES~~-~~, including the location of the areas of highest supply (hotspots); and ii) assess the impact of the level of analysis on the relationships (potential trade-offs and synergies) among different ES, and between ES and forest biodiversity. We compare three levels of spatial resolution: local (~1 km^2), municipality and county, using 10 indicators, including seven ES (food and water provision, climate regulation, soil fertility, flood regulation, erosion control and recreation), forest cover and two biodiversity measures (woody plants and bird species richness). Our study area is a highly populated and environmentally diverse Mediterranean region in Catalonia (NE of Iberian Peninsula). In comparison with other regions in the Mediterranean context, the study area shows high forest cover and population density, and a wide variety of forest types due to the marked altitudinal and climatic gradient in this region.

2. Material and methods

2.1. Study area

Our study area is Catalonia (NE of Spain; Figure 1), an administrative region covering 32,114 km^2 and mainly located in the Mediterranean biogeographic region. Catalonia and its subregional administrations have shared political responsibilities in planning and managing biodiversity and ES. Catalonia has a population of 7.5 million people, most of them living in or around the capital city (Barcelona). It is a mountainous area with an altitudinal range from the sea level to more than 3,000 meters. It is a highly forested region (43% of its area is covered by forests), with the main tree species belonging to the genera *Pinus* and *Quercus*. The forests from coastal and low altitude areas are dominated by *Pinus halepensis* and *Quercus ilex*. At mid-altitudinal ranges –from 800 to 1,500 m- the main species are *P. sylvestris*, *P. nigra*, *Q. humilis* and *Q. faginea* and also *Fagus sylvatica* in the wettest zones. Finally, at altitudes higher than 1,500 m the main species are *P. uncinata* and *Abies alba*. The study area is divided in 41 counties (average extension = 783.1 km^2, range = 114.7 - 1784.1 km^2) and 947 municipalities (average extension = 33.9 km^2, range = 0.6 - 302.8 km^2).

2.2. Data sources

In this work, we analysed the spatial patterns of a series of seven ES indicators (food and water provision, climate regulation, soil fertility, flood regulation, erosion control and recreation) and additional descriptors of forest cover and biodiversity (woody and bird species richness) at three different spatial scales: local (1-km^2 cells or forest inventory plots), municipality and county. Two sources of information were particularly important for estimating these indicators. On the one hand, the Third Spanish National Forest Inventory (SNFI; MAGRAMA 1997-2007), which provides detailed, plot-level information of forest characteristics, with a sampling density of one plot every ~1 km^2 of forest area. The SNFI records species identity, height and diameter at breast height (DBH) of all living and standing dead trees on circular plots of variable radius depending on tree size (5 m radius for trees with DBH $\geq$ 7.5 cm, 10 m radius for trees with DBH $\geq$ 12.5 cm, 15 m radius for trees with DBH $\geq$ 22.5 cm and 25 m radius for trees with DBH $\geq$ 42.5). On the other hand, the Land Cover Map of Catalonia (LCMC, 2009) was used to obtain high resolution thematic cartography of the land cover of Catalonia. It is a vector map generated by photo-interpreting on 1:5000 colour ortho-photo images, with a minimum patch area of 500 m^2, a working spatial scale of 1:1000, a pixel resolution of 0.25 meters and 241 different legend categories.

2.3. Description and calculation of forest ES indicators

We worked with seven indicators of three main groups of ES (i.e., provisioning (P), cultural (C) and regulating (R)), following widely used ES classifications (e.g. CICES (Haines-Young and Potschin, 2012). We also assessed two biodiversity indicators and a measure of forest cover. All these indicators are described briefly in the following paragraphs; more detailed information can be found elsewhere (Roces-Díaz et al., 2017b).

Mushroom production (P1, food provision, Provisioning ES) was estimated for each SNFI plot using the models developed by de-Miguel et al. (2014) for the study area. These models were developed based on the monitoring, from 1995 to 2012, of weekly mushroom production from permanent sample plots representing most pine forest ecosystems throughout the study region, i.e., pure and mixed stands of *P. sylvestris*, *P. nigra*, *P. halepensis* and *P. pinaster*. Mixed-effects models based on site and stand characteristics were used to estimate the potential production of edible mushrooms of commercial interest for a typical year, in $kg\cdot ha^{-1}\cdot year^{-1}$. In the study area edible mushrooms occur primarily in pine forests.

Exported water (P2, water provision, Provisioning ES) was calculated also for each SNFI plot using the water balance model developed by de Cáceres et al. (2015) for the study area. This model provides information on the amount of water exported (blue water, in $L\cdot m^{-2}\cdot year^{-1}$) from each forest plot based on the physical properties of soil, climate and forest composition and structure.

Number of animal observations (C1, recreation, Cultural ES) per 1 km^2 forest cell was calculated using the data from the web portal of the Catalan Ornithological Institute (Sardà-Palomera et al., 2012; Herrando-Moraira et al., 2016), www.ornitho.cat storing more than 3,000,000 observations. Bird watching is an important recreational activity in the study area. Data represents observations of animal species (including birds, mammals, reptiles, amphibians and some groups of invertebrates), and consists of observations uploaded by users of the mentioned webpage all around Catalonia between 2010 and 2015. Only those cells where the forest cover was dominant (>50% of the total area) were included in further analyses.

Carbon sequestration (R1, climate regulation, Regulating ES) was calculated following Vayreda et al. (2012) as the carbon stock change in each SNFI plot (in $t \cdot ha^{-1} \cdot year^{-1}$) between two consecutive surveys (2nd and 3rd SNFI survey)). In Catalonia, the 2nd SNFI was conducted in 1990 and the 3rd SNFI in 2000, so the period between surveys of a given plot was ~10 years.

Soil organic Carbon (SOC; R2, soil fertility, Regulating ES) was estimated as the average value of Carbon stored in soil ($t \cdot ha^{-1}$) obtained from the map of soil organic carbon of Spain (Doblas-Miranda et al., 2013). This map provides the SOC content on a grid with a cell size 200 x 200 m. It is based on more than 900 field samples that were used to build a multiple regression model with environmental data (climate, vegetation cover) as independent variables. Only those cells where the forest cover was dominant (>50% of the total area) were included in further analyses.

Riparian forest cover (R3, flood regulation, Regulating ES) was calculated as the percentage of area along rivers (50 m width buffer) that is covered by forest in each 1x1 km cell (according to the LCMC). Only those cells where river occurrence was relevant (the buffers around rivers covered >5% of the pixel area) were used in further analyses.

Forest cover in slopes (R4, erosion control, Regulating ES) shows the percentage of landscape with a slope ≥ 30% that is covered by forest, in each 1x1 km cell, based on the original 0.25 m cells of the LCMC. Only those cells where the forest cover was dominant (>50% of the total area) were included in further analyses.

2.4. Calculation of additional forest descriptors

Woody plant richness (B1, Biodiversity) represents the number of different woody species detected in each SNFI plot, municipality or county, based on the information collected in the third SNFI survey.

Forest bird richness (B2, Biodiversity) correspond the number of forest bird species estimated on each 1 x 1 km cell, municipality or county. The data was based on the second Catalan Breeding Bird Atlas (Estrada et al. 2004). Fieldwork was conducted between 1999 and 2002 and represents a total of 3,077 cells of 1 km^2 resolution. Presence/absence data for breeding bird species and environmental predictors were used to develop species distribution models and a cross-validation procedure was applied for the assessment of model performance.

Forest cover (F1) represents the percentage of area of each level (1x1 km cell, municipality or county) covered by forest ecosystems.

2.5. Data analyses

Most indicators (mushrooms production, exported water, number of animal observations, carbon sequestration and soil organic carbon) were scaled up to the municipality and county levels by averaging the point or grid data values at 1 km^2 resolution. To reduce methodological artefacts, the variables that were computed as a percentage of forest cover (riparian forest cover, forest cover in slopes and forest cover) were calculated directly from raw data at the municipality and county levels. Finally, biodiversity variables always corresponded to the total number of different species (woody species for B1 or forest birds for B2) detected at each spatial scale (plot/grid cell, municipality or county).

Some original variables were transformed by using square root or logarithmic functions to normalize their distribution prior to analysis. However, some variables could not be normalized (see table 1 for specific information on the transformation used for each variable).

As our main objectives was to assess the spatial pattern of ES, hotspots and spatial autocorrelation analyses were performed only for the seven ES indicators. The analyses were performed using ArcGIS 10.2 (ESRI, 2011). The hotspots analysis was conducted separately at the three spatial levels of analysis. The hotspot areas of each indicator were calculated using two different methods depending on the data type (point data from SNFI plots or grid data). For the point data, hotspots were defined following a clustering method based on the Getis-Ord Gi* statistic (Getis and Ord, 1992; Ord and Getis, 1995), which is appropriate to feature data types (Schröter and Remme, 2015). This statistic is calculated as (eq.1):

$$G_i^* = \frac{\sum_{j=1}^{n} w_{i,j} x_j - \left[\frac{\sum_{j=1}^{n} x_j}{n}\right] \sum_{j=1}^{n} w_{i,j}}{S \sqrt{\frac{\left[n \sum_{j=1}^{n} w_{i,j}^2 - \left(\sum_{j=1}^{n} w_{i,j}\right)^2\right]}{n-1}}} \qquad \text{Eq.1}$$

Where n is the number of spatial features; $w_{i,j}$ is the distance between features i and j; x_j is the value of each ES indicator, and S is calculated as follows (eq.2):

$$S = \sqrt{\frac{\sum_{j=1}^{n} x_j^2}{n} - \left[\frac{\sum_{j=1}^{n} x_j}{n}\right]^2} \qquad \text{Eq.2}$$

For a given dataset, the Getis-Ord Gi* statistic identifies those clusters of spatial features with values of ES supply higher than those expected by random chance we represented those features identified as hotspots with 95% of probability. For the grid data, the calculation of the Getis-Ord Gi* statistic is not possible. Therefore, we defined hotspots as those areas that represented the highest values of supply (the cells where the supply was >80% percentile; Schröter and Remme, 2015). In order to quantify the differences produced by the delimitation of hotspot areas at the three spatial levels, we compared the percentage overlap between these areas at the different spatial scales.

Differences in spatial patterns of ES indicators among the three levels of analysis were further inspected using Spatial Autocorrelation. Firstly, Moran´s I coefficient (Moran, 1948) (eq.3) was calculated for the patterns of each ES indicator at the three different levels:

$$I = \frac{n}{\sum_{i=1}^{n}\sum_{j=1}^{n} w_{i,j}} \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} w_{i,j} z_i z_j}{\sum_{i=1}^{n} z_i^2} \qquad \text{Eq.3}$$

Where n is the number of spatial features; $w_{i,j}$ is the distance between features i and j; z_i and z_j are the deviation of the attribute (here the value of each indicator) for feature i and j, respectively, from the mean value. This index allowed determining the spatial clustering of the ES indicators at the three levels of analysis. Secondly, Incremental Spatial Autocorrelation (ISA) was used for estimating spatial autocorrelation at increasing distances. This method is also based on the calculation of Moran´s I coefficient using a moving window size. For our analyses window size ranged from 1,000 (based on minimum distance among plots) to 126,000 meters, with an increment of 5,000 m. This range of values used was similar to a previous application of this methodology on the analysis of ES patterns (Roces-Díaz et al., 2017a).

To analyse possible trade-offs and synergies between ES and forest variables (table 1) we calculated Pearson and Spearman correlations between pairs of variables at the three different levels of analysis (Mouchet et al., 2014). We calculated these correlations (Pearson for those involving variables with normal distribution and Spearman for those involving at least one variable we could not normalize; cf. Table 1) by using the R statistical software (v.3.2.5; R Development Core Team, 2016).

Finally, to explore in more detail the relationships between the ES indicators and biodiversity and forest cover we fitted linear models at the different levels: local, municipality and county. We used woody species richness (B1), bird richness (B2) and forest cover (F1) as independent variables and the ES indicators as dependent variables. We assessed multi-collinearity among explanatory variables by calculating Variance Inflation Factors (VIF), which were always < 1.5, confirming that multi-collinearity was not an issue in our models. For local and municipal level we fitted linear mixed-effects models with municipality nested in county (local level) or county (municipality level) as random factors. For the county level we fitted standard linear models. The residuals of these models did not show any obvious pattern and their distribution was approximately normal (Supplementary material Appendix A). In all statistical analyses significance was accepted whenever the p-value < 0.05.

3. Results

3.1. Spatial distribution of biodiversity variables, forest cover and ES indicators

Forest cover and forest biodiversity variables showed differences in their spatial patterns at the three levels analysed (Figure 2). In all three cases, relatively high values of forest cover (F1), woody species richness (B1) and bird richness (B2) found at the local level in southern areas of the study region progressively disappeared at coarser spatial scales (municipality and county), for which highest values clustered more and more towards the northern part of the study area.

The distribution of ES indicators was more conservative and showed broadly similar patterns at the three levels of analysis (Figures 3 and 4). Thus, those areas that showed higher supply values at local levels also tended to present high supply at municipality and county levels. However, some differences among these levels can also be highlighted. For example, exported water (P2) and erosion control (R4) showed some of the highest values at local level in the north-east of the study area, but this pattern disappeared at coarser scales (Figures 3 and 4). Overall, most ES indicators showed highest values towards the north of the study area at all levels, with the exception of animal observations (C1), which were clustered along the vertical corridor linking Barcelona to the French border. Some indicators (e.g., carbon sequestration, R1 and riparian forest, R3) showed a scattered, fine-grained pattern with high supply zones across all the study area, which was highly eroded at the county level.

3.2. Characterization of ES spatial patterns

Spatial patterns of hotspots areas showed marked differences among the different ES indicators (Figure 5). Overall, most ES indicators hotspots were located on the northern half of Catalonia.

However, two indicators (animal observations and riparian forest) presented their hotspots more uniformly distributed across all the forests in the study area. Some remarkable differences were detected among levels of analysis. While some indicators showed highly overlapping hotspots at the three levels (e.g., mushroom production, exported water or soil organic carbon), the hotspots of other indicators were clearly disjoint across scales. This was particularly the case for ES indicators showing scattered hotspot patterns distributed over most of the study area at local level (animal observations and riparian forest). In those cases, the fine grained spatial distribution of hotspots was generalized at coarser scales and hotspots tended to concentrate towards the north of the study area. The percentage of spatial agreement of hotspots at the three levels is shown in Table 2. Mushroom production, exported water, soil carbon and erosion control presented a high level of correspondence across scales (~90% agreement or higher between local and municipality levels, >70% between local and county levels). At the other extreme, animal observations and riparian forest presented much lower overlaps, in the order of 50% or lower, across spatial scales. Overall, the level of agreement was higher between local and municipality levels than between local and county levels, with the only exception of wildlife observations.

All ES indicators showed substantial spatial autocorrelation, characteristic of clustered patterns (Supplementary material Appendix B). Moran´s I coefficient showed higher values for most of the ES indicators when the level of analysis increased (0.07-0.61 for the local level; 0.26-0.63 for municipality; and 0.17-0.69 for county). In a similar way, incremental spatial autocorrelation analysis showed differences in the spatial aggregation patterns among levels of analysis for the seven ES indicators (Figure 6). Local and municipality levels showed similar aggregation patterns, with maximum spatial autocorrelation at distances between 1,000 and 11,000 meters. However, the situation was very different at the county level, which showed maximum spatial autocorrelation at distances >31,000 m, reflecting the larger characteristic size of these spatial units.

The pair-wise relationships between ES indicators, and among ES indicators and forest cover and biodiversity variables, were generally positive and significant, indicating a preponderance of synergies over trade-offs (Table 3). The strongest and most consistent relationships across scales were those between mushroom production, exported water, soil carbon and erosion control. Interestingly, the value of most correlation coefficients increased from local to county levels. In particular, negative (and significant) relationships were only observed at the local level, most of them between woody species richness and some ES indicators, such as mushroom production, exported water, soil carbon and erosion control. These negative relationships disappeared at municipality and county levels, where they shifted to positive (but not always significant) correlations (Table 3). Thus, some potential trade-offs detected at the finest spatial resolution were not detected, or even became positive, potentially synergistic effects, at coarser spatial scales.

Linear models of ES indicators as a function of forest cover and biodiversity variables also showed substantial differences among levels of analysis (Table 4), which were generally consistent with the results obtained from the correlation analysis. Thus, some explanatory variables showed significant negative effects at local level but not at municipality or county levels (e.g., woody species richness on mushroom production and exported water). Interestingly, the negative relationship of woody species richness with soil carbon remained significant at the three spatial scales according to the corresponding linear models. Bird richness showed generally positive (and significant) relationships with most of the indicators. The local effect of forest cover could be either positive (mushroom production, soil organic carbon, erosion control) or negative (animal observations, riparian forest), and tended to decline at larger spatial scales. Finally, the explained variance (model R^2) varied among ES indicators, with R^2 (standard or conditional depending on model type) being ≥ 0.32 in all cases except for animal observations and carbon sequestration, for which the explained variance was much lower (Table 4). Scatter-plots among forest descriptors and ES indicators at three levels are showed in supplementary material.

4. Discussion

4.1. Influence of the spatial level of analysis on ES patterns and hotspots areas

At the international level, different policies are integrating ES approaches in biodiversity conservation and environmental management strategies (e.g., EU Biodiversity Strategy to 2020). Although this integration requires the use of specific methodologies for the accurate mapping and characterization of ES (Maes et al., 2012), spatial ES assessments frequently show inconsistencies and mismatches, which often result in relatively high uncertainty (Crossman et al., 2013; Hou et al., 2013; Geijzendorffer et al., 2015). Among these sources of uncertainty, those derived from scale effects are particularly important because they underlie the identification of ES spatial patterns, which is critical when ES assessments are translated into land-use or management decisions (Xu et al., 2017).

Our results confirmed the influence of scale of analysis on the distribution patterns of different ES indicators. These results appear logical considering the scale-dependency of the ecological processes underlying ES provision (Hein et al., 2006) and are consistent with previous findings showing the influence of spatial data characteristics (e.g., spatial, temporal or thematic resolution) on ES patterns (Konarska et al., 2002; Kandziora et al., 2013; Gret-Regamey et al., 2014), including indicators of the supply, demand and flow of ES (e.g., Bagstad et al., 2014; Wolff et al., 2015). Although it is known that the spatial level of analysis may influence ES assessments (Geijzendorffer et al., 2015), the number of works assessing the importance of this effect is still limited (e.g., Raudssep-Hearne and Peterson, 2016) and most ES assessments are based on the use of administrative (or similar) boundaries including municipalities, counties or larger levels (referred generically as NUTS (Nomenclature of territorial units for statistics) Rodriguez-Loinaz et al., 2015; Roces-Díaz et al., 2017b; Schulp et al., 2014).

In our study, the level with finest resolution (local) was based on 1-km^2 cells, and provides a similar level of detail to previous works that assessed similar sets of ES for comparable study areas (e.g., Anderson et al., 2009; Eigenbrod et al., 2010; Locatelli et al., 2013). In general, ES indicators showed relatively heterogeneous spatial patterns, which turned into more homogeneous patterns at coarser spatial scales. This is a recognized effect of spatial aggregation (Levin, 1992; Constanza and Maxwell, 1994), with consequences for data interpretation and the corresponding management decisions: while in some instances generalization may be a necessary (and desirable) means of dealing with high spatial variability, the resultant averaging effect can dismiss important fine-grained information.

The distribution of ES indicators and the corresponding hotspots showed higher agreement between the local and municipality levels of analysis than between the local and the county levels. Although this agreement was less marked for those ES with scattered spatial patterns (i.e., animal observations and riparian forest), it shows that the analysis at the municipality level reflected better the variability provided by fine-grain information and is more accurate than the analysis at coarser administrative levels. The incremental spatial autocorrelation (ISA) analysis, which showed similar spatial patterns at the local and municipality levels, but highly distinct patterns at the county level, also supported this notion. Our results are generally consistent with previous work exploring how spatial patterns of ES hotspots are affected by spatial resolution (Eigenbrod et al., 2010; Homolova et al., 2014) and how spatial autocorrelation of ES patterns depends on spatial resolution (Gret-Regamey et al., 2014). The municipality level can be highlighted as a convenient scale for ES analysis that allows to integrate indicators from a multiplicity of data sources (e.g., Raudsepp-Hearne et al., 2010; Rodriguez-Loinaz et al., 2015; Roces-Díaz et al., 2017b) and, at the same time, provides relatively accurate spatial patterns.

4.2. Spatial relationships and influence of analysis level

The spatial level of analysis also influenced the relationships between pairs of ES indicators, and between them and forest cover and biodiversity variables. Our results confirm how these processes, including trade-offs and synergies between ES, are dependent on spatial scales (Rodriguez et al., 2006). It is well recognized that the implementation of the ES approach on land planning and natural resources management needs an accurate assessment of these types of effects at different scales, as previous research has shown that administrative boundaries can affect their identification (Deng et al., 2016). In this regard, we found that an increase in the spatial level of analysis can mask potential trade-offs among ES, particularly when local data are compared with aggregated indicators at broader scales (i.e. municipality or county). These findings are in agreement with previous works (e.g., Yang et al., 2015; Liu et al., 2017) where fewer trade-offs (and more synergies) among ES were detected at larger compared to finer scales.

In general, our results showed stronger correlations at lower spatial resolution (municipality/county levels), in agreement with other works where the influence of spatial levels of analysis on trade-offs/synergies was explored (Anderson et al., 2009; Xu et al., 2017). Although most indicators/variables showed consistent relationships across scales (cf. Raudsepp-Hearne and Peterson, 2016), some of them presented contrasted relationships at local vs. coarser scales. This was particularly the case of woody species richness, which showed negative and significant correlations (i.e. potential trade-offs) with several ES indicators, including regulating and provision ES, at the local level that turned into positive correlations (i.e. potential synergies) at coarser spatial scales. This mismatch indicates the importance of landscape heterogeneity (gamma vs. local, alpha diversity) in supporting high levels of ES supply, and it is consistent with the notion that coarser scales may describe a spatial mosaic arrangement that allows several ES to concur at the landscape level synergically (e.g. in a multifunctional rural landscape).

The negative relationships obtained between woody species richness and ES contrast with many studies showing consistently positive relationships between biodiversity and ES (Egoh et al., 2009; Harrison et al., 2014; Strassburg et al., 2010), but agree with other works focused on forest ES (i.e., Locatelli et al., 2013; Lautenbach et al., 2017). Most of the ES indicators for which negative relationships with biodiversity were found are highly dependent on climatic productivity (mushroom production in de-Miguel et al., 2014; exported water in de Caceres et al., 2015; soil organic carbon in Doblas-Miranda et al., 2013). In the study area, these areas with high productivity often involve historically managed forests that are characterized by low tree richness (frequently monospecific stands focused largely on timber production (Onaindia et al., 2013; Rodriguez-Loinaz et al., 2013).

Although linear models generally confirmed the presence of some negative relationships between ES indicators, particularly at the local level, they were generally more consistent across spatial scales than simpler correlation analyses. This result suggests that some of the inconsistencies across scales might be explained by covariance with third variables. Overall, our results highlight the importance of assessing relationships among ES at different spatial and temporal scales (Tomscha and Gergel, 2016) to obtain a robust (and interpretable) characterization of potential trade-offs and synergies between them.

4.3. Main strengths and limitations

The two coarser spatial scales that we used correspond to administrative boundaries often used for land use planning and management, and are thus directly relevant from an applied perspective. In addition, the set of ES indicators (and biodiversity variables) used in this work is based on the combination of field and environmental data (as recommended by Martinez-Harms et al., 2016) that account, whenever possible, for the underlying ecological processes. Finally, the indicators we have chosen provide information on different types of forest ES and include those believed to be more relevant in the study area.

On the other hand, this study has a series of potential limitations that should be highlighted. Firstly, the local analysis level is based (for some indicators such as for example soil organic carbon or erosion control) on regular grids, while municipality and county levels are derived from administrative boundaries that involved a wide range of sizes and shapes. Thus, differences on spatial patterns among these levels could be influenced by these inherent differences in shape and distribution. In addition, the combination of several data sources allowed analysing a wide range of ES. However, some of these indicators derived from primary data, while others were based on ecological deterministic models or land use maps, and differences in data sources and estimation approaches may affect spatial patterns (Eigenbrod et al., 2010; Martínez-Harms et al., 2016). Finally, to provide a consistent set of ES indicators at the three spatial levels of analysis, some of them had to be obtained using relatively simplified approaches (compare for example with the indicators developed in Guerra et al. (2016) for erosion control).

5. Conclusions

We explored the effect of using different spatial scales and administrative boundaries on ES assessment and mapping. We report substantial information loss when coarser spatial scales (county level) were used, whereas spatial patterns at the local and municipality level remained similar. Some trade-offs among ES and between ES and biodiversity were only detected at the local scale, implying that caution is needed when interpreting relationships between ES at relatively coarse spatial scales. Following this, the use of high-resolution-data (when available) is recommended, in particular when identifying hotspots areas or trade-offs/synergies are of primary interest. In more descriptive assessments in which the main objective is describing broad spatial patterns of ES distribution, intermediate levels (municipality) are also adequate, as they conserve many of the spatial properties of assessments conducted at finer spatial scales and have the advantage of being more directly relevant for policy-making.

Supplementary material

Appendix A shows the residuals of the linear models fitted at different spatial scales.

Appendix B shows the results of Spatial Autocorrelation tests.

Appendix C shows scatter-plots among forest descriptors (biodiversity and forest cover variables) and ES indicators at the three spatial levels of analysis.

Acknowledgments

We thank to the volunteers from the Catalan Ornithological Institute (ICO) and Dr. Miquel de Cáceres Ainsa for providing data for the analyses presented in this study. Funding was obtained from the Catalan Office for Climate Change (OCCC) through project ForESMap, from EU FORESTERRA program (INFORMED project) and from the Spanish government (CGL2013-46808-R and AGL2015-66001-C3-1-R). JVRD was supported by the Government of Asturias and the FP7-Marie Curie-COFUND program of the European Commission (Grant 'Clarín' ACA17-02). We also thank the ECOMETAS (CGL2014-53840-REDT) network for support. This study also received funding from the European Union's Horizon 2020 research and innovation programme within the framework of the MultiFUNGtionality Marie Skłodowska-Curie Individual Fellowship (IF-EF) under grant agreement No655815 and from the Generalitat de Catalunya (Serra-Hunter Fellow). We thank Gabriel Borras and Gemma Cantos (OCCC) for useful discussion during the elaboration of this work. We are very grateful to all persons who made the two Spanish Forest Inventories possible and, especially, to their main coordinators, Ramon Villaescusa (IFN2) and Jose Antonio Villanueva (IFN3). We also thank two anonymous reviewers who helped us improve the quality of the manuscript.

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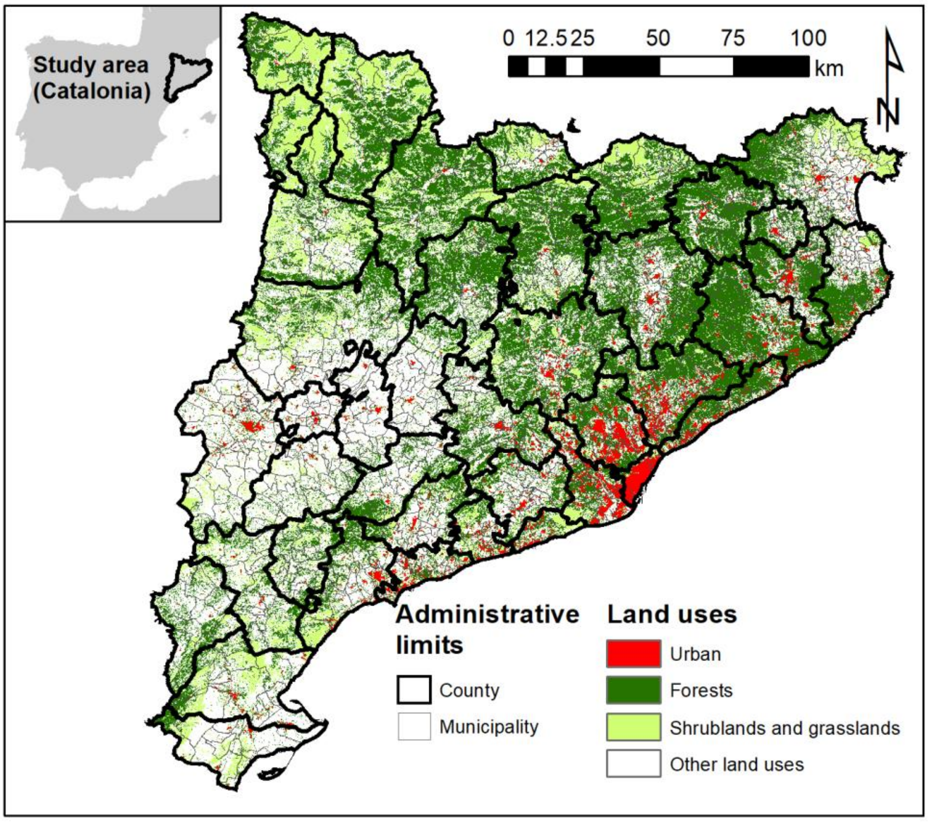


Figure 1. Location of the study area, including the different administrative limits (municipality and county) and main types of land cover (LCMC, 2009).

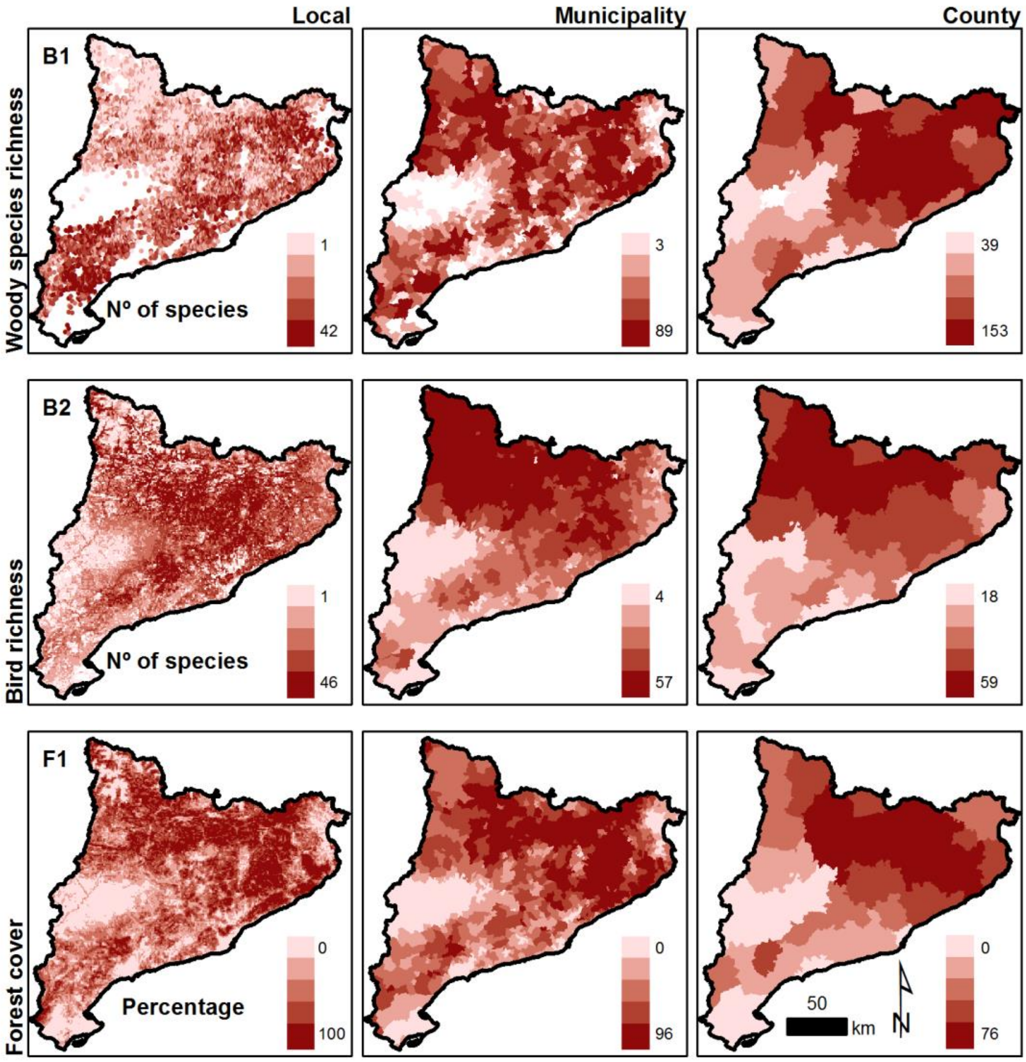


Figure 2. Spatial patterns of biodiversity (woody species richness (B1) and bird richness (B2)) and forest cover (F1) in Catalonia at the three levels of analysis (local, municipality and county) used in this work. Colour intensity indicates increasing, 20% percentile classes.

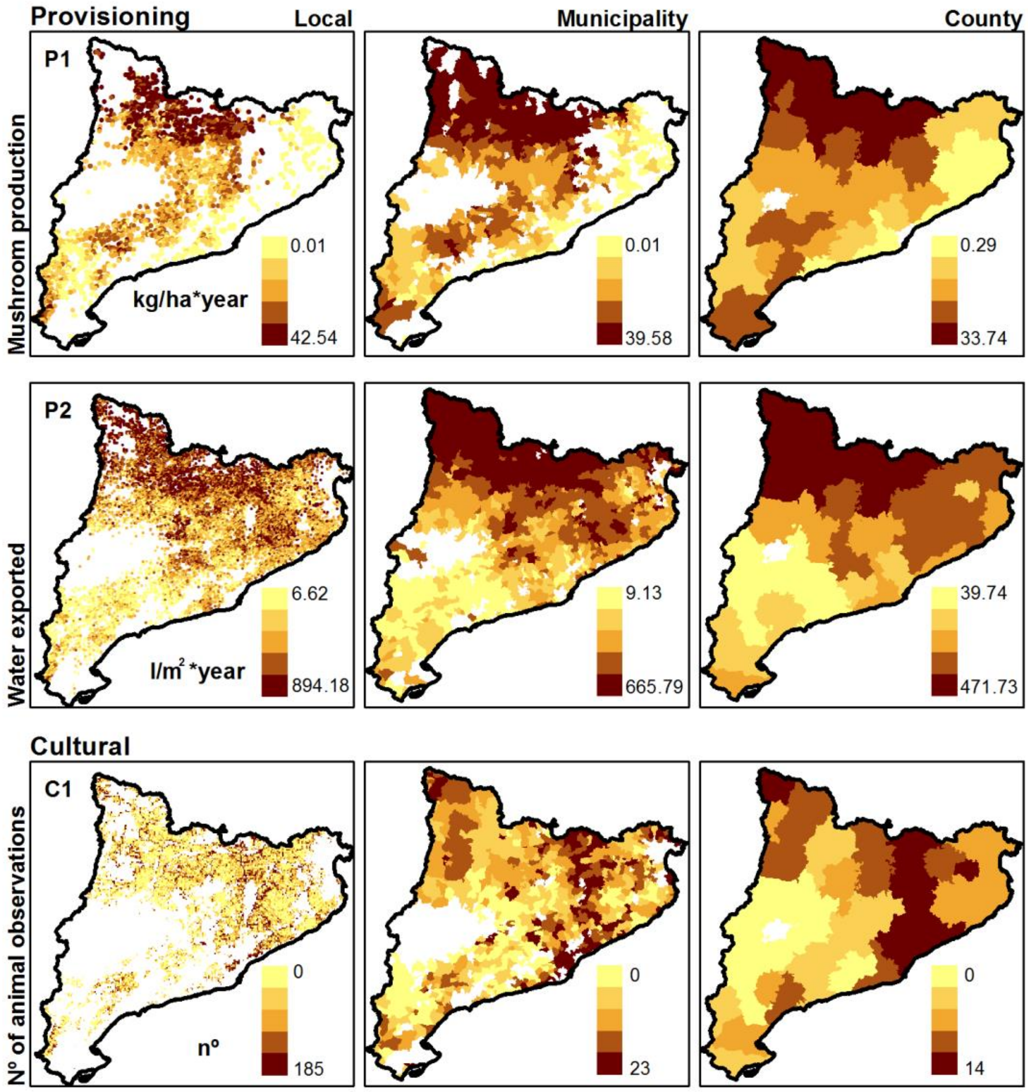


Figure 3. Spatial patterns of provisioning ES (mushroom production (P1) and water exported (P2)) and cultural ES (animal observations (C1) indicators in Catalonia at the three levels of analysis (local, municipality and county) used in this work. Colour intensity indicates increasing, 20% percentile classes.

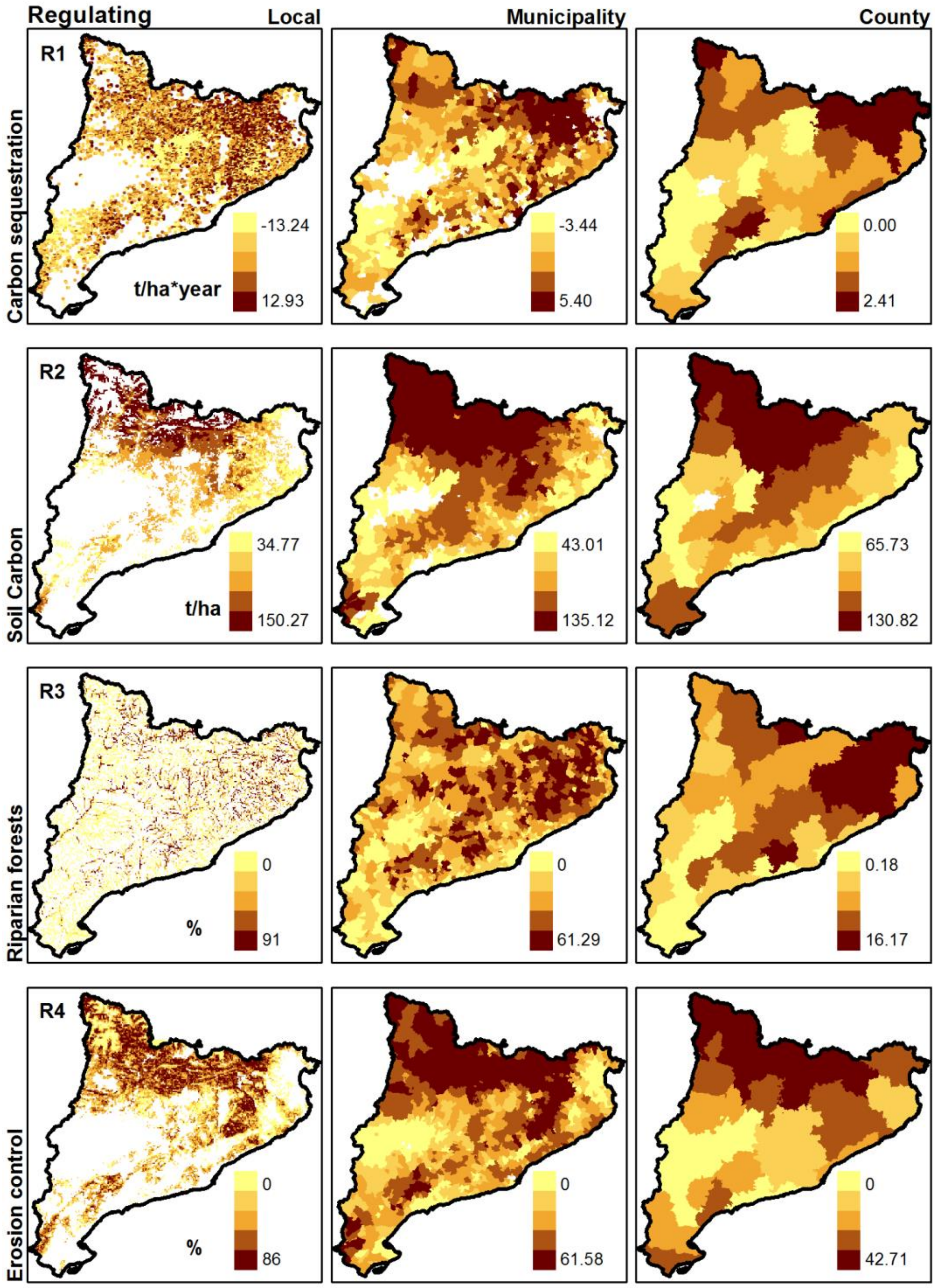


Figure 4. Spatial patterns of regulating ES (carbon sequestration (R1), soil organic carbon (R2), riparian forest (R3) and erosion control (R4)) indicators in Catalonia at the three levels of analysis (local, municipality and county) used in this work. Colour intensity indicates increasing, 20% percentile classes.

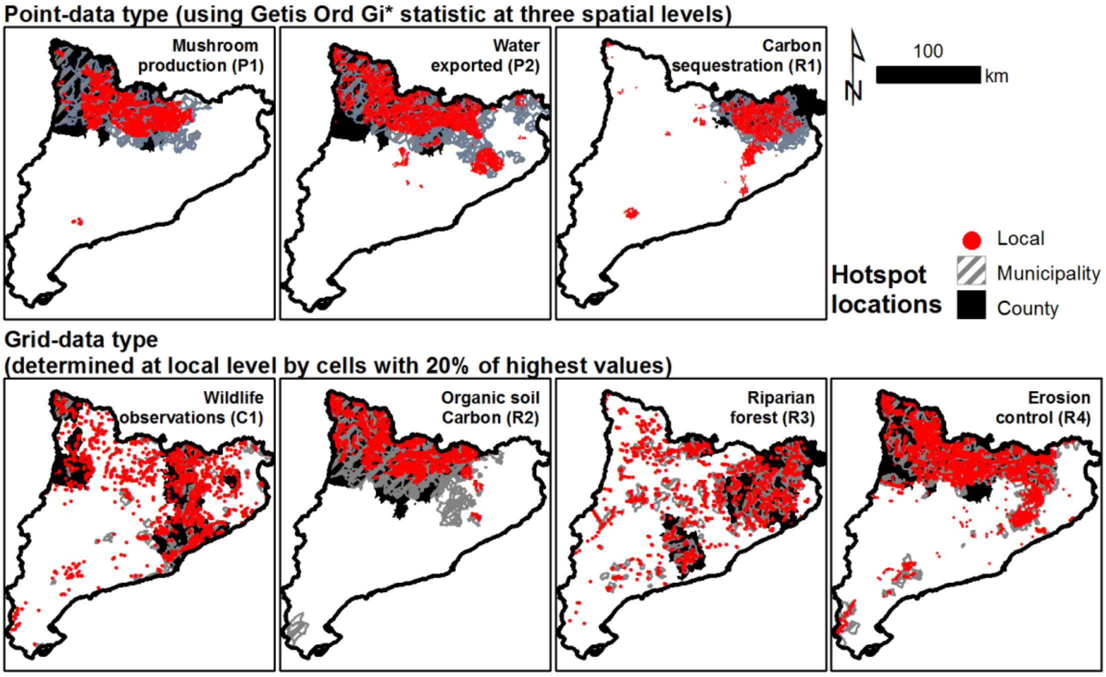


Figure 5. Spatial patterns of hotspots of ES indicators at the three levels of analysis (local, municipality and county) used in this work.

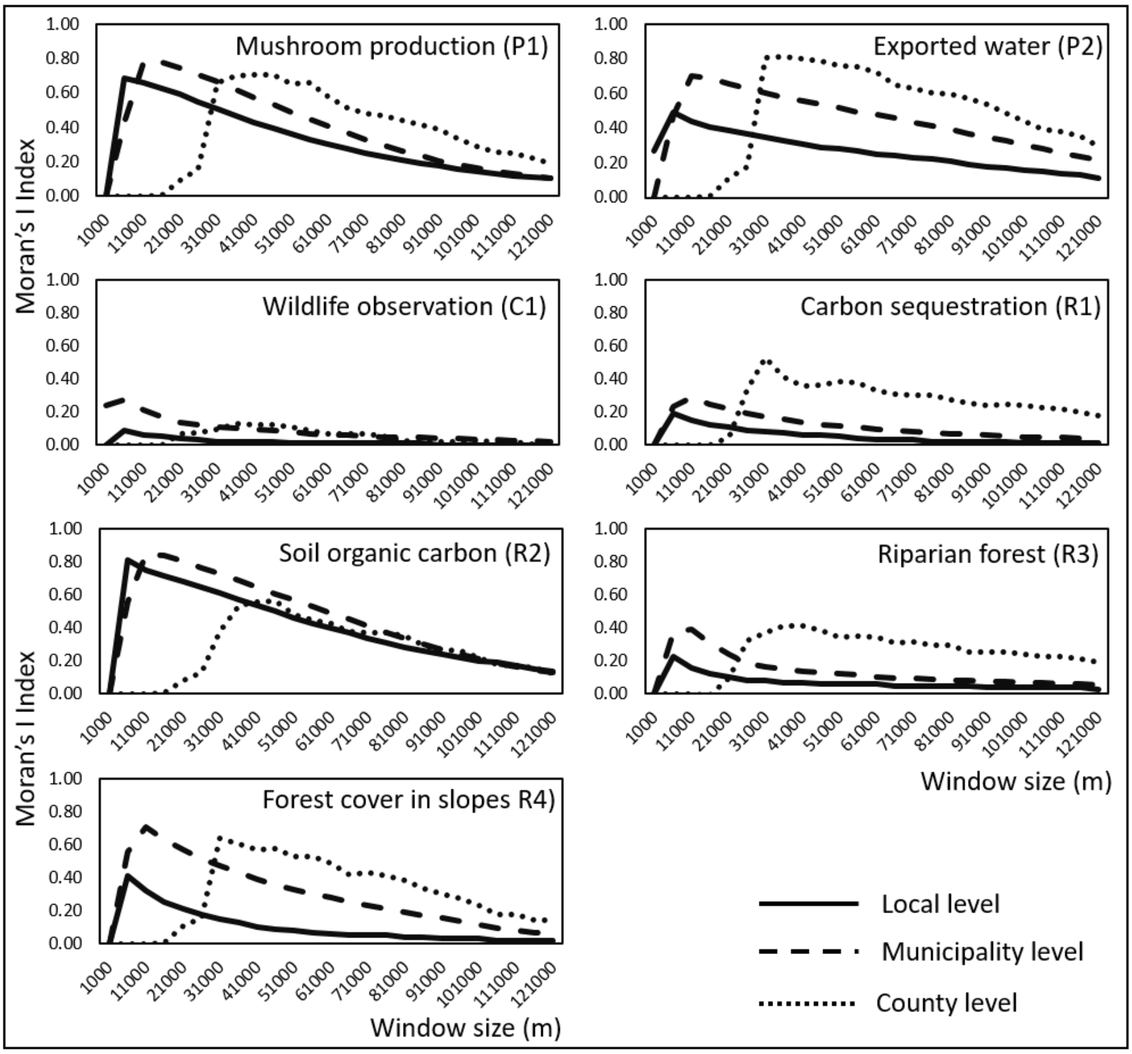


Figure 6. Results of Incremental Spatial Autocorrelation analysis that shows values of Moran´s I index (vertical axis) from increasing sizes of windows (horizontal axis; meters).

Tables

Table 1. Description of the main variables used in this work. The transformations used to normalize the distribution of the variables were: root square (sqr) or logarithmic (ln). Normalization showed if each variable was (or not) normalized. Two different types of correlation coefficients were used: Pearson and Spearman (when the variable could not be normalized). Further details are provided in the text.

Category	ES/ variable	Indicator	Code	Units	Data	N/original resolution	Transform.	Normal.	Sources
Forest Biodiversity	Tree diversity	Woody species richness	B1	Nº	Point (SNFI plot)	11,288 plots	sqr(x)	Yes	MAGRAMA (1997-2007)
	Bird diversity	Forest bird richness	B2	Nº	Grid	1,000 m	-	No	ICO (2014)
Forest cover	Forest cover	Forest cover	F1	%	Grid	25 m	ln(x+0.1)	Yes	LCMC (2009)
Provisioning Ecosystem Services	Food provision	Mushrooms	P1	kg/ha/year	Point (SNFI plot)	3,272 plots	sqr(x)	Yes	de-Miguel et al. (2014)
	Water provision	Exported water	P2	L/m^2/year	Point (SNFI plot)	11,261 plots	sqr(x)	Yes	de Caceres et al. (2015)
Cultural Ecosystem Services	Recreation	Wildlife observation	C1	Nº	Grid	1,000 m	ln(x+0.1)	No	ICO (2014)
Regulating Ecosystem Services	Climate regulation	Carbon sequestration	R1	t/ha/year	Point (SNFI plot)	8,726 plots	sqr(x)	Yes	Vayreda et al. (2012)
	Soil fertility	Soil organic Carbon	R2	t/ha	Grid	200 m	-	Yes	Doblas-Miranda et al. (2013)
	Flood regulation	Riparian forest cover	R3	%	Grid	25 m	ln(x+0.1)	No	LCMC (2009)
	Erosion control	Forest cover in slopes	R4	%	Grid	25 m	sqr(x)	No	LCMC (2009)

Table 2. Percentage of hotspots at local level included inside the hotspot areas at municipality and county levels.

		Ecosystem Services indicators [a]						
	Direction of change	**P1**	**P2**	**C1**	**R1**	**R2**	**R3**	**R4**
% of local hotspots included at higher levels	**Local to municipality**	98.1	92.9	38.8	74.2	98.9	53.7	88.0
	Local to county	72.8	75.3	52.2	61.3	97.2	48.2	71.5

[a] Ecosystem services indicators: Mushrooms (P1), Exported water (P2), Wildlife observation (C1), Carbon sequestration (R1), Soil organic Carbon (R2), Riparian forest cover (R3), Erosion control (R4).

Table 3. Correlation coefficients between pairs of environmental variables and ES indicators (*: p-value < 0.05). Red colours: significant negative relationships and green colours: significant positive relations

Local		B2	F1	P1	P2	C1	R1	R2	R3	R4
Woody sp. rich.	B1	0.02	-0.06*	-0.41*	-0.47*	-0.02	-0.01	-0.44*	0.07*	-0.32*
Bird richness	B2	1	0.79*	0.20*	0.08*	0.28*	0.18*	0.05*	0.13*	0.12*
Forest cover	F1		1	0.42*	0.12*	-0.18*	0.24*	0.06*	0.18*	0.47*
Mushroom prod.	P1			1	0.53*	0.03	0.13*	0.82*	-0.01	0.53*
Exported water	P2				1	0.07*	0.11*	0.48*	0.05*	0.34*
Animal obs.	C1					1	0.06*	0.06*	0.09*	0.02
Carbon seq.	R1						1	0.04	0.13*	0.12*
Soil Carbon	R2							1	-0.14*	0.49*
Riparian forest	R3								1	0.03
Erosion control	R4									1
Municipality		**B2**	**F1**	**P1**	**P2**	**C1**	**R1**	**R2**	**R3**	**R4**
Woody sp. rich.	B1	0.50*	0.69*	0.23*	0.10	-0.06	0.14*	0.28*	0.17*	0.55*
Bird richness	B2	1	0.73*	0.54*	0.65*	0.24*	0.29*	0.69*	0.47*	0.70*
Forest cover	F1		1	0.37*	0.34*	0.06	0.33*	0.47*	0.37*	0.79*
Mushroom prod.	P1			1	0.43*	0.13*	0.00	0.81*	0.04	0.61*
Exported water	P2				1	0.30*	0.14*	0.48*	0.27*	0.39*
Animal obs.	C1					1	0.23*	0.13*	0.00	0.19*
Carbon seq.	R1						1	0.23*	0.24*	0.24*
Soil Carbon	R2							1	0.23*	0.56*
Riparian forest	R3								1	0.20*
Erosion control	R4									1
County		**B2**	**F1**	**P1**	**P2**	**C1**	**R1**	**R2**	**R3**	**R4**
Woody sp. rich.	B1	0.71*	0.83*	0.16	0.58*	0.38	0.56*	0.35	0.69*	0.56*
Bird richness	B2	1	0.81*	0.57*	0.83*	0.47*	0.44	0.70*	0.61*	0.80*
Forest cover	F1		1	0.25	0.69*	0.54*	0.45	0.47*	0.72*	0.69*
Mushroom prod.	P1			1	0.53*	0.09	0.15	0.88*	0.18	0.65*
Exported water	P2				1	0.51*	0.49*	0.64*	0.50*	0.75*
Animal obs.	C1					1	0.58*	0.31	0.19	0.54*
Carbon seq.	R1						1	0.38	0.46*	0.51*
Soil Carbon	R2							1	0.36	0.75*
Riparian forest	R3								1	0.42
Erosion control	R4									1

Table 4. Linear models for the seven ES indicators as dependent variables and the three biodiversity and forest cover indicators as independent variables. Local and municipality level analyses correspond to mixed-effects models and county level analyses were conducted using simple linear models. Local level models used municipality (nested in county) and county as random factors; municipality level models used county as random factor. Significance level *** <0.001; **<0.01, *<0.05; -<0.1. R2m: marginal R-squared, R2C: conditional R-squared, R2: R-squared; SE: standard error.

Indicators	**Spatial level**	**Intercept**		**Woody sp. richness (B1)**		**Bird richness (B2)**		**Forest cover (F1)**		**R-squared**		
		Coef.	**SE**	**Coef.**	**SE**	**Coef.**	**SE**	**Coef.**	**SE**	**R2m**	**R2c**	**R2**
Mushrooms Production (P1)	Local	0.112	0.952	-0.338***	0.064	0.001	0.004	0.914***	0.202	0.027	0.798	-
	Municip.	-1.889***	0.517	0.049	0.041	0.048***	0.011	0.655***	0.116	0.153	0.808	-
	County	-1.676	1.3	-0.356-	0.194	0.209***	0.038	-0.553	0.564	-	-	0.44
Water Exported (P2)	Local	18.062***	3.831	-1.843***	0.256	0.031*	0.014	-0.13	0.832	0.062	0.53	-
	Municip.	5.087***	1.273	-0.01	0.107	0.179***	0.027	-0.003	0.296	0.149	0.753	-
	County	-6.791*	2.741	-0.793	0.408	0.523***	0.081	0.628	1.189	-	-	0.64
Wildlife observations (C1)	Local	8.187***	1.437	-0.16	0.096	0.034***	0.005	-2.114***	0.313	0.132	0.356	-
	Municip.	-1.43***	0.416	0.021	0.042	0.042***	0.009	-0.12	0.112	0.114	0.341	-
	County	-1.404-	0.784	-0.16	0.117	0.019	0.023	0.646-	0.34	-	-	0.14
Carbon sequestration (R1)	Local	1.086**	0.416	-0.026	0.028	0.003*	0.002	0.03	0.09	0.01	0.184	-
	Municip.	0.369**	0.141	-0.024	0.014	0.009***	0.003	0.099	0.039	0.1	0.363	-
	County	0.12	0.288	0.008	0.043	0.014	0.008	0.024	0.125	-	-	0.14
Soil organic Carbon (R2)	Local	81.911***	7.506	-4.462***	0.493	-0.069*	0.027	5.136**	1.573	0.044	0.871	-
	Municip.	50.872***	4.998	-1.395***	0.404	0.775***	0.104	3.114**	1.113	0.161	0.817	-
	County	19.399	13.05	-6.946**	1.94	2.613***	0.385	2.276	5.661	-	-	0.61
Riparian forest (R3)	Local	3.146	2.321	0.296	0.154	0.052***	0.009	-1.394**	0.506	0.085	0.317	-
	Municip.	-2.389***	0.649	0.106	0.065	0.059***	0.014	0.124	0.181	0.149	0.392	-
	County	-3.804***	0.833	0.294	0.124	0.027	0.025	0.307	0.362	-	-	0.53
Erosion Control (R4)	Local	-10.93***	1.89	-0.233	0.128-	0.024***	0.007	3.551***	0.411	0.07	0.62	-
	Municip.	-5.162***	0.661	0.102	0.061-	0.055***	0.014	1.708***	0.170	0.381	0.677	-
	County	-2.185*	0.918	-0.078	0.137	0.119***	0.027	0.456	0.398	-	-	0.59

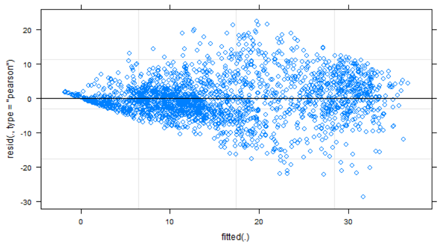
The spatial level of analysis affects the patterns of forest ecosystem services supply and their relationships

Supplementary material.

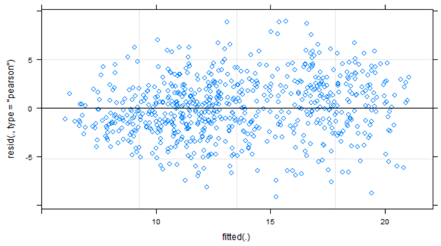
Appendix A. Residuals of the linear models fitted at different spatial scales.

Local level (mixed-effect models)

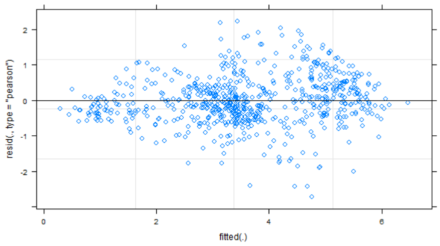
P1 (mushroom production)



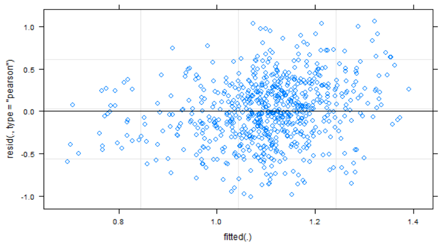
P2 (exported water)



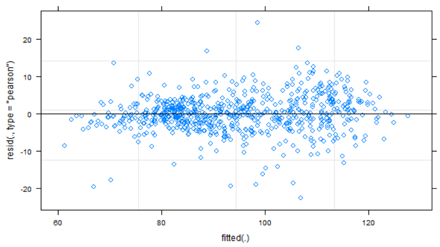
C1 (wildlife observation)



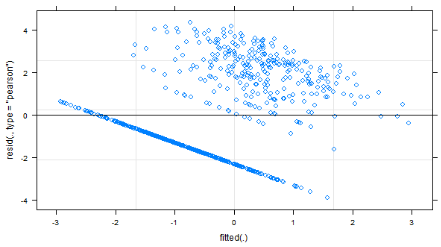
R1 (carbon sequestration)



R2 (soil organic carbon)



R3 (riparian forest)



R4 (forest cover in slopes)

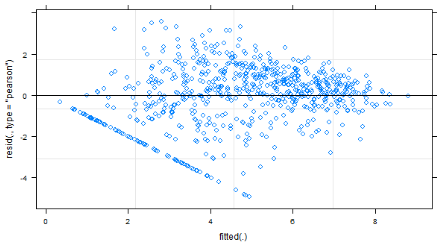
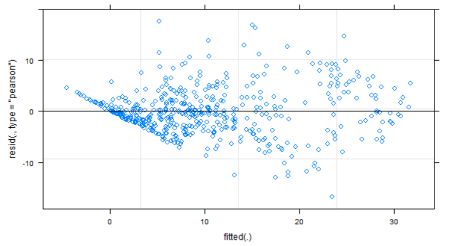


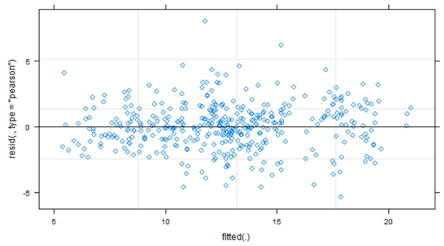
Figure S1. Residuals of mixed-effect models for ES indicators at local level.

Municipality level (mixed-effect models)

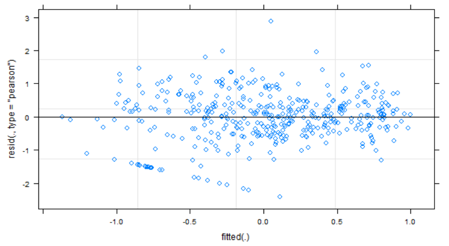
P1 (mushroom production)



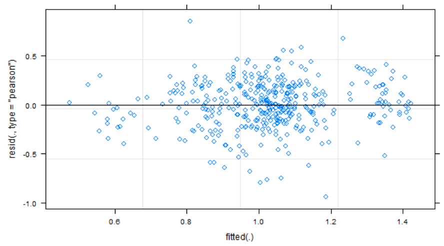
P2 (exported water)



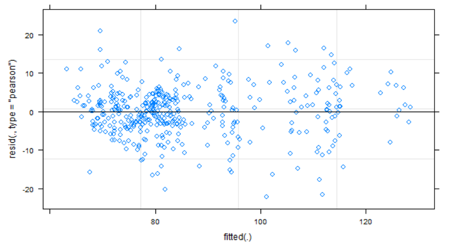
C1 (wildlife observation)



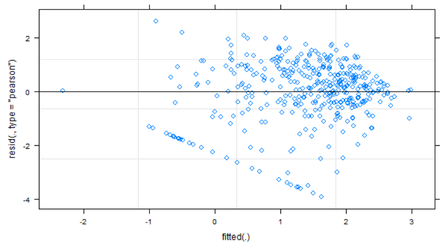
R1 (carbon sequestration)



R2 (soil organic carbon)



R3 (riparian forest)



R4 (forest cover in slopes)

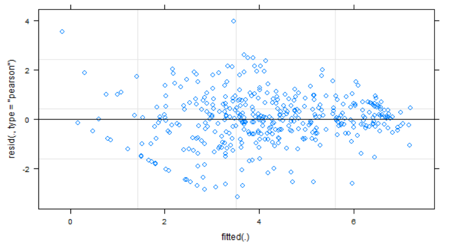
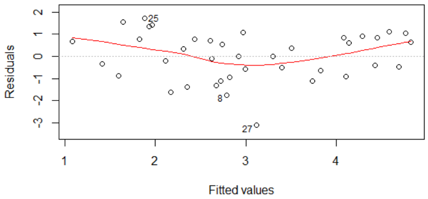


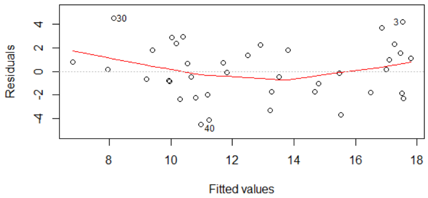
Figure S2. Residuals of mixed-effect models for ES indicators at municipality level.

County level (general linear models)

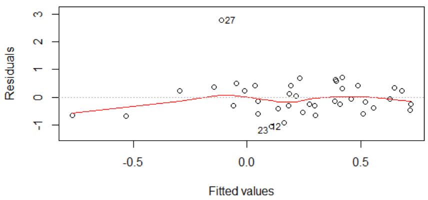
P1 (mushroom production)



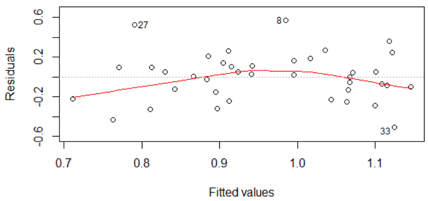
P2 (exported water)



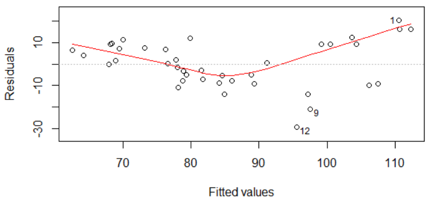
C1 (wildlife observation)



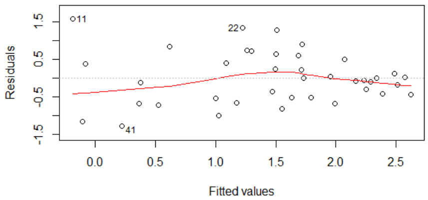
R1 (carbon sequestration)



R2 (soil organic carbon)



R3 (riparian forest)



R4 (forest cover in slopes)

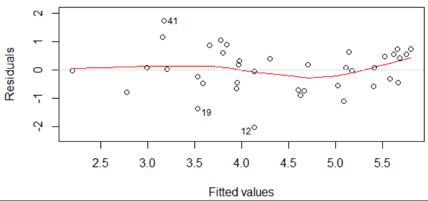


Figure S3. Residuals of general lineal models for ES indicators at county level.

Appendix B. Results of spatial autocorrelation tests.

Table S1. Spatial autocorrelation results.

ES indicator	Level	Moran´s I coefficient	Z score	p-value
Mushroom production	Local	0.61	261.24	< 0.01
	Municipality	0.63	45.24	< 0.01
	County	0.51	3.85	< 0.01
Exported water	Local	0.41	284.78	< 0.01
	Municipality	0.53	40.43	< 0.01
	County	0.69	5.31	< 0.01
Wildlife observation	Local	0.07	74.07	< 0.01
	Municipality	0.45	23.69	< 0.01
	County	0.17	2.82	< 0.01
Carbon sequestration	Local	0.19	127.58	< 0.01
	Municipality	0.26	19.13	< 0.01
	County	0.46	3.59	< 0.01
Soil organic carbon	Local	0.37	386.28	< 0.01
	Municipality	0.61	19.19	< 0.01
	County	0.52	4.03	< 0.01
Riparian forest	Local	0.36	100.11	< 0.01
	Municipality	0.49	35.97	< 0.01
	County	0.35	2.84	< 0.01
Forest cover in slopes	Local	0.41	423.21	< 0.01
	Municipality	0.56	41.41	< 0.01
	County	0.52	4.11	< 0.01

Appendix C. Scatter-plots among forest descriptors (biodiversity and forest cover variables) and ES indicators at the three spatial levels of analysis.

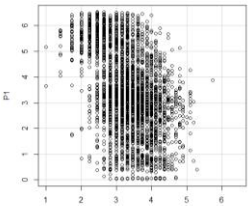
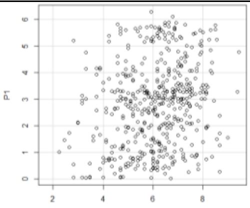
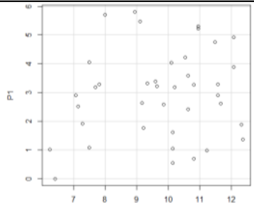
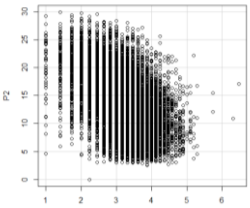
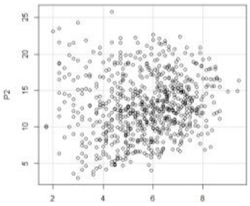
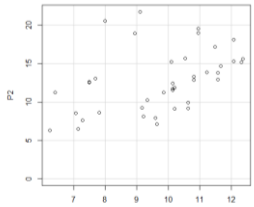
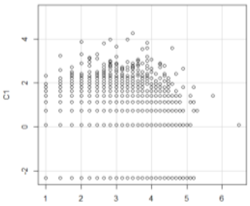
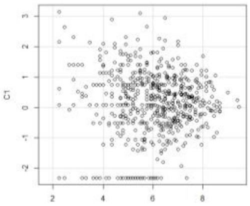
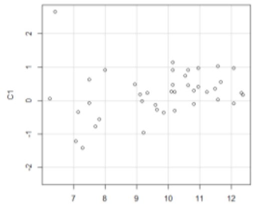
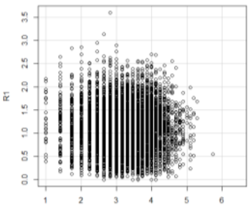
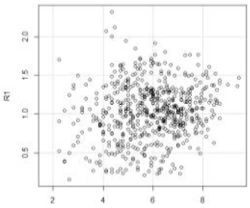
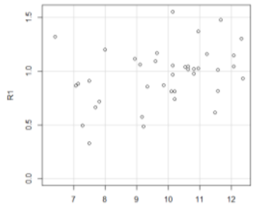
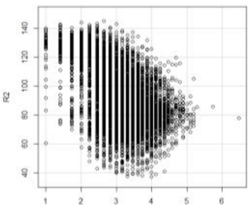
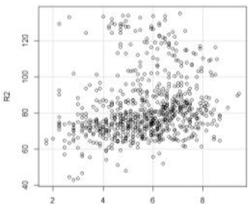
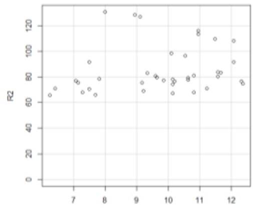
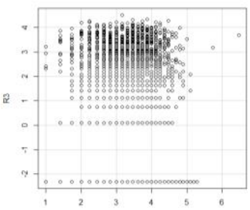
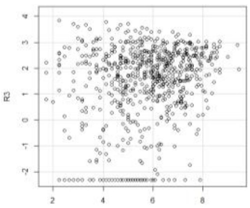
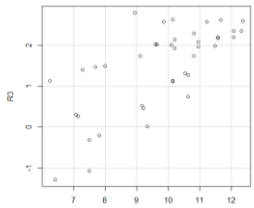
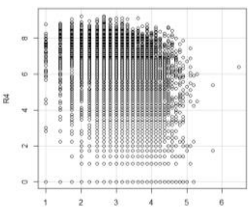
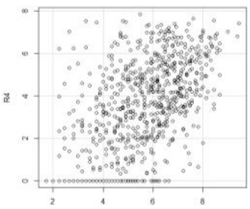
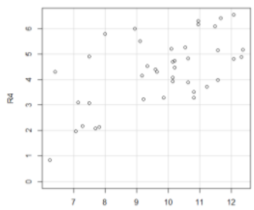
Dependent Variables	Local	Municipality	County
Mushroom Production (kg/ha/year) srq(x)	 *	 *	
Exported Water ($L/m^2/year$) srq(x)	 *		 *
Animal Observations (Nº) ln(x+0.1)			
Carbon Sequestration (t/ha/year) srq(x)		 *	 *
Soil Carbon (t/ha)	 *	 *	
Riparian Forest (%) ln(x+0.1)	 *	 *	 *
Erosion Control (%) sqr(x)	 *	 *	 *

Figure S4. Scatter-plots between woody species richness (square root transformed, X-axis) and ES indicators (*: p-value < 0.05). Units of dependent variables and their transformations (if any) are showed in the first column.

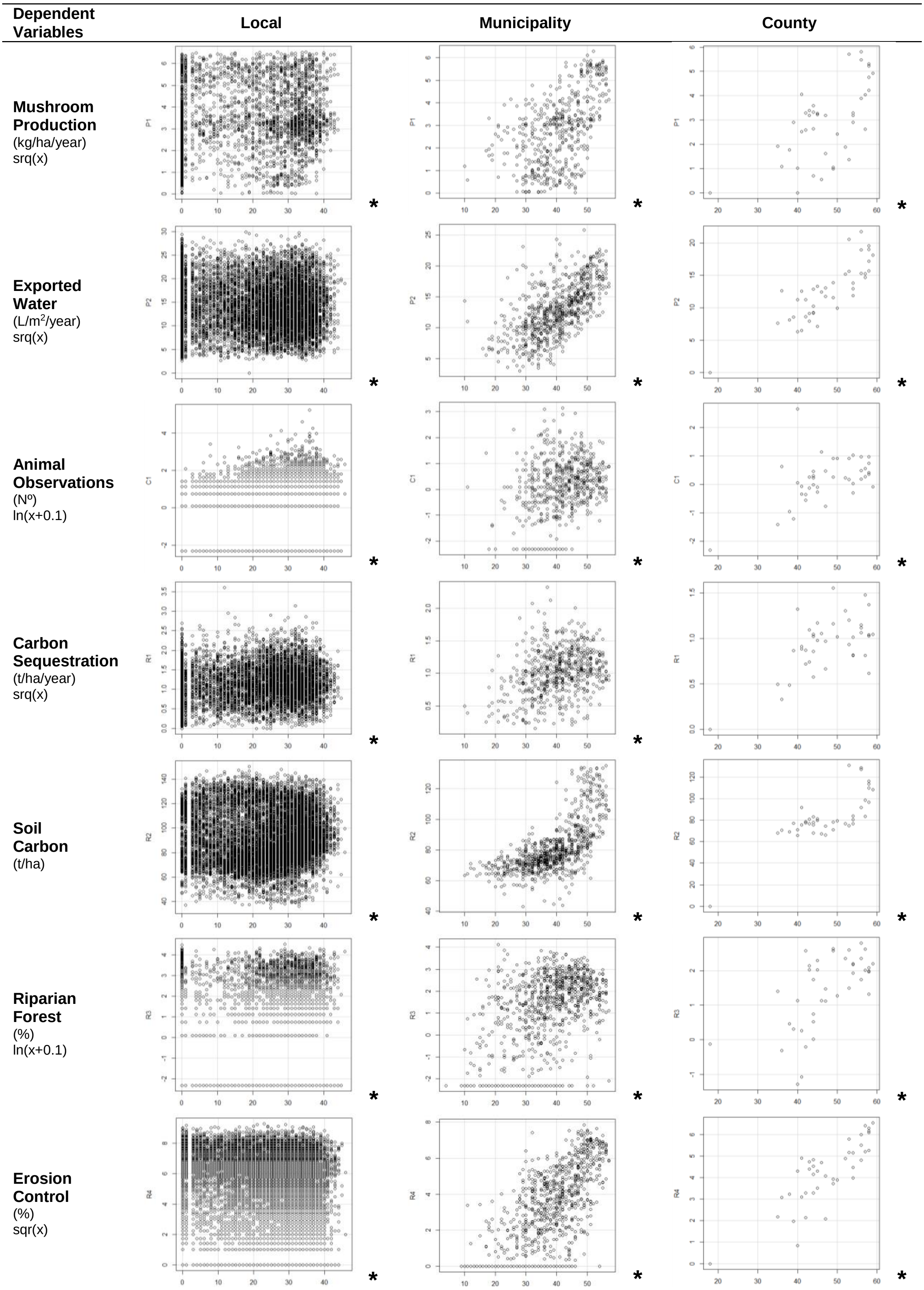


Figure S5. Scatter-plots between bird species richness (X-axis) and ES indicators (*: p-value < 0.05). Units of dependent variables and their transformations (if any) are showed in the first column.

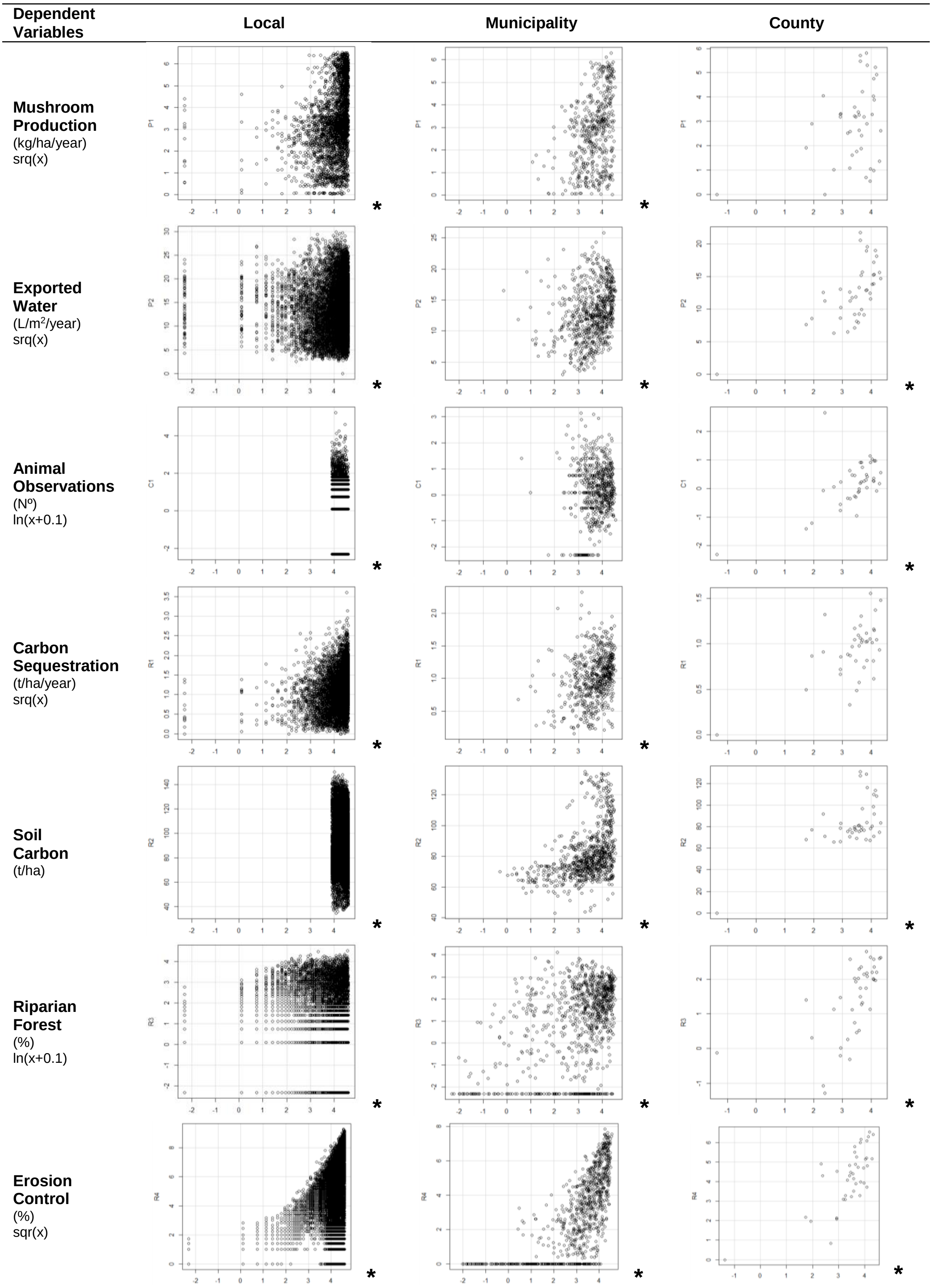


Figure S6. Scatter-plots between forest cover (X-axis; transformation: ln (forest cover + 0.1) and ES indicators (*: p-value < 0.05). Units of dependent variables and their transformations (if any) are showed in the first column.