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Effect of forest management on the ecosystem services supply and multifunctionality in the Urdaibai Biosphere Reserve ☆

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ABSTRACT

Forest ecosystems provide a wide range of ecosystem services (ES) that are essential for human well-being. Nevertheless, conventional forest management practices that prioritise timber production often reduce the capacity of forests to provide a balanced set of other ES, thereby diminishing their overall multifunctionality. The aim of this study is to develop a field-based multi-indicator methodological approach to assess how different forest management types influence the multifunctionality value based on the supply of thirteen ES (two provisioning, nine regulating and two cultural), and to identify the forest attributes (location, structure and maturity, and soil properties) that influence the provision of each ES. The research was conducted in the Urdaibai Biosphere Reserve, a relevant protected area of the Basque Country (Spain). The forest management types selected for the study were as follows: i) *No managed* native forests, ii) *Abandoned* pine plantations, iii) *Pine managed* plantations, and iv) *Eucalyptus managed* plantations, with 10 stands sampled for each management type. The findings indicated that *No managed* and *Abandoned* exhibited higher multifunctionality value and greater values in regulating and cultural ES in comparison to managed plantations, which supplied higher timber provision, yet exhibited suboptimal performance in other ES. The application of generalised linear mixed models has revealed a positive correlation between forest attributes, including soil pH and vertical heterogeneity, and the provision of multiple ES. However, it has also been observed that slope has a negative effect on certain regulating ES. These findings underscore the significance of forest management practices that preserve both the structural complexity of the forest and landscape, whilst simultaneously enhancing soil conditions to ensure multifunctionality. Furthermore, abandoned pine plantations have the potential to demonstrate ecological restoration, thereby supporting natural regeneration and improving the delivery of regulating and cultural ES.

1. Introduction

In recent centuries, the European landscape has undergone drastic structural changes, with natural habitats being lost or reduced in size and fragmented, and urban areas expanding (Haddad et al., 2015; Pedroli and Meiner, 2017). These changes have significant implications for climate change effects, biodiversity loss, and the degradation of ecosystem services (ES). A salient transformation in the EU landscape is the expansion fast-growing exotic species in forest plantations, which poses a threat to native species and modifies forest structure and species composition, frequently leading to a decline in biodiversity and an impact on ES (FAO, 2020). Forests represent multifunctional ecosystems, which play a significant role in global biodiversity conservation whilst providing a wide range of ES to society (Cardinale et al., 2012). These include provisioning ES (e.g. timber provision), regulating ES (e.g. water regulation, carbon storage, and erosion control), and cultural ES (e.g. recreation and traditional knowledge). It is evident that all of these ES contribute to human well-being and sustainable economic

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development (Costanza et al., 2017).

In Europe, approximately 80 % of forests have been managed or are actively managed, with specific management practices implemented based on forest conditions and the objectives of the forest owners or managers (Winkel et al., 2022). Historically, forest management practices have prioritised timber production, resulting in a decline in biodiversity and a reduction in the capacity of forests to provide other essential ES (McGrath et al., 2015, Helseth et al., 2022). In order to optimise production, managers have focused on the expansion of even-aged and homogeneous stands, which are dominated by a limited number of tree species (FAO, 2020; Betts et al., 2021). This approach has resulted in a reduction in the aesthetic and recreational value of the forests (Peura et al., 2016), as well as limitations in terms of pest control and habitat maintenance (Jactel and Brockerhoff, 2007; Calviño-Cancela et al., 2012). Furthermore, direct management effects, including thinning and harvesting operations, have been demonstrated to alter forest structure (Ehbrecht et al., 2021), soil characteristics, and the amount of deadwood. These changes have the potential to affect a range of ES (Felipe-Lucia et al., 2018). Exploring alternative management strategies that enhance forest multifunctionality is particularly important for increasing its capacity to adapt to changing environmental conditions. Such alternatives benefit from considering the forest attributes that influence the provision of ES (Vadell et al., 2022).

In this particular context, multifunctionality has been defined as "the simultaneous provision of multiple ecosystem functions or ES". Various methods exist for quantifying it. On the one hand, maps of multiple ES supplies are often overlapped to identify ES bundles or hotspots that can be prioritised for conservation (Chan et al., 2006; Ortega et al., 2023). Conversely, trade-offs between ES are calculated to enhance the pluralistic value of the ES (Himes et al., 2020) or to select the scenarios that maximise multifunctionality in forest plantations (Schwaiger et al., 2019; Blattert et al., 2020, Caicoya et al., 2023). However, the majority of these approaches have adopted a landscape-level perspective, relying on data from national forest inventories (Helseth et al., 2022), complex models (Schwaiger et al., 2019; Blattert et al., 2020), or scenario analyses, including climate, management, or policy scenarios (Caicoya et al., 2023). While valuable, these approaches frequently show a strong dependency on site-specific characteristics (Schwaiger et al., 2019) and are less suited to capture the dynamics of smaller forested regions. This limitation is particularly relevant in protected areas and fragmented landscapes, where land ownership is highly divided and stakeholders often have competing priorities for ES (e.g., timber production *versus* regulating services). As a result, there is a clear knowledge gap regarding field-based, *in situ* approaches that can evaluate the effects of forest management on multifunctionality in small, fragmented regions (Juerges et al., 2021).

In the north-west of the Iberian Peninsula, *Pinus radiata* D. Don and *Eucalyptus* spp. have been commonly used in forest plantations, owing to their high profitability. However, different researches have indicated that such exotic species can exert adverse impacts on local biodiversity and ES provision (Castro-Díez et al., 2021). *Pinus radiata* has been extensively planted in Galicia and the Basque Country due to its rapid growth and adaptability to the local climatic conditions (Turner et al., 2001). However, it has been demonstrated that this species can also induce changes in soil properties and increase soil erosion (Edeso et al., 1999). This phenomenon can be attributed to a variety of factors, including unsustainable management practices (Ainz, 2008), and the slow decomposition of pine needles, leading to the accumulation of organic matter and disruption of nutrient cycling (Barraqueta and Basagoiti, 1988; Cifuentes-Croquevielle et al., 2020). Moreover, pine plantations are particularly vulnerable to certain pine-specific diseases and pests (Brockerhoff et al., 2023), such as the red band and brown spot needle diseases that have affected pine plantations in the Basque Country and other regions in the last decades (Monteiro et al., 2022; Ortuño et al., 2022). The aforementioned diseases have had a substantial impact on the profitability of pine plantations, resulting in their replacement with eucalyptus plantations or even to the abandonment of pine plantations, as observed in other regions of the Iberian Peninsula (Vaz et al., 2019). However, the abandonment of pine plantations may present a valuable opportunity for the restoration of native forests, as these areas can serve as catalysts for the regeneration of plant species characteristic of these ecosystems (Onaindia et al., 2013b). This, in turn, could enhance forest resilience and contribute to climate change mitigation efforts (Allek et al., 2023).

Conversely, *Eucalyptus* spp. plantations, predominantly situated in Portugal and Galicia, have recently expanded into the Basque Country, where their environmental impacts remain inadequately studied (Elosegi et al., 2020; Sertutxa et al., 2024). However, in other regions, studies have shown that eucalyptus plantations can decrease nutrient and water availability in soils (Amazonas et al., 2018; Hoogar et al., 2019) and reduce biodiversity compared to native forests (Riffo-Donoso et al., 2021). Consequently, approximately one-third of forestry sector stakeholders have expressed concerns regarding the environmental impacts of eucalyptus plantations, including soil degradation, water scarcity, loss of native species, and vulnerability to pests. These stakeholders also emphasise the necessity for further information regarding the consequences of planting these species (Zafra-Calvo et al., 2024).

In recent decades, there has been an increased interest in the ES approach within protected areas, as these areas have been found to be more effective in supplying ES compared to exploited areas (Hummel et al., 2019). However, in order to facilitate effective policy decisions and sustainable forest management in these areas, it is essential to establish a robust theoretical foundation, understand prevailing trends, and assess the implications of various management strategies (Carpenter et al., 2006). The objective of this study is to develop a field-based multi-indicator methodological approach to assess how different forest management types influence the multifunctionality value based on the supply of thirteen ES, and to identify the forest attributes that influence the provision of each ES. While the Urdaibai Biosphere Reserve (UBR) in the Basque Country serves as a pilot case, this framework has been designed to be transferable to other regions, where it will facilitate the evaluation of the consequences of different management strategies and provide evidence to support forest policy-making and guide sustainable forest management.

This research is particularly relevant to the ongoing development of the new provincial forestry regulation in Bizkaia, which seeks to strengthen forest protection and restoration, enhance sustainable management, and promote decentralised forest monitoring and planning to ensure resilient and multifunctional forest ecosystems. This regulation is expected to be aligned with the objectives of the EU Forest Strategy for 2030, which emphasises the promotion of multifunctional, climate-resilient forests that contribute to the bioeconomy and biodiversity conservation. Given that the Basque forestry sector remains a major economic driver, achieving a balance between ecological, social, and economic objectives is essential, and requires effective, evidence-based forest and environmental management.

2. Methods

2.1. Study area

The UBR is a protected area in the Basque Country that is of significant ecological importance, with a total area of 22,000 ha. The area was designated a Biosphere Reserve in 1984, owing to its inherent natural and cultural value, and was subsequently incorporated into the European Union's Natura 2000 network. This has facilitated the ecological conservation of the area and the sustainable socio-economic development of the territory, resulting in a complex socio-ecological system characterised by the intersection of economic interests and nature conservation (Onaindia et al., 2013a). Subsequently, in 1993, a strategic plan was proposed for the exploitation of its natural resources, while respecting the management and conservation of nature (Basque

Government, 2004).

The potential vegetation of UBR corresponds to acidophilic Atlantic mixed forests belonging to the *Hyperico pulchri-Querco roboris sigmetum* series, but these only occupy 9 % of the territory. In contrast, forest plantations of exotic species (*Pinus radiata* D. Don and *Eucalyptus* spp.) occupy 50 % of the area (Castillo-Eguskitza et al. 2017), and are located mainly on small private properties. The majority of Atlantic mixed forests are characterised by fragmentation, coming from secondary forests regenerating following the abandonment of crops and meadows, a process that has taken place for over 40 years. These ecosystems are found at altitudes below 600 m and are characterised by acid soils with a pH between 3.5 and 6, formed from non-carbonate rocks, such as sandstone, quartzite, and granite (Loidi et al., 2011). Moreover, a wide diversity of flora and fauna of high ecological interest can be found in these and other ecosystems, such as in the Cantabrian holm oak forests or in the estuary with its marshes.

2.2. Stand selection

A total of ten stands, each with an area exceeding 1 ha, were selected at random for each forest management type within the UBR: native Atlantic mixed forests that have not been managed (*No managed*); old pine plantations that have been abandoned (*Abandoned*); pine plantations with medium-rotation (30–35 years) management (*Pine managed*); and eucalyptus plantations with short-rotation (15–20 years) management (*Eucalyptus managed*). A total of 40 stands were sampled (see Fig. 1). For verifying the close to harvesting developmental stage of stands, orthophotos were employed for both the *Pine managed* and *Eucalyptus managed* stands. For stands designated as *Abandoned*, orthophotos were utilised to ascertain that they were in an abandonment stage (>45 years). In the latter, field visits were conducted to confirm the absence of recent management activities. This selection process ensured a representative sampling of the four forest management types, allowing for robust comparisons of ES supply and multifunctionality.

2.3. Forest attributes and ES selection

The direct effects of management, such as thinning and harvesting operations, have been shown to alter average tree size, canopy cover, vertical heterogeneity or the amount of deadwood, all of which are likely to be important for different ES (Felipe-Lucia et al., 2018). Moreover, other ES may be more responsive to underlying environmental factors, such as soil properties or slope (Spielvogel et al., 2009), which are known to capture site-specific characteristics. Therefore, ten forest attributes were selected, including forest location (slope and diversity of the surrounding landscapes), forest structure (vertical heterogeneity, the diameter at the breast height (DBH) and tree density), forest maturity (volume of deadwood in early and late decay stages, and the diversity of decay stages), and soil properties (organic matter content and pH).

In the same way, thirteen ES previously identified in the UBR (Onaindia et al., 2010; Onaindia et al., 2015) were selected for further analysis. These services encompass provisioning services, which include food and timber provision, as well as regulating services, which encompass habitat maintenance, climate regulation, air quality regulation, water regulation, soil erosion control, soil fertility maintenance, biological control (pest and disease control), and regulation of extreme events. In addition, cultural services, namely traditional knowledge and recreation, are also included (Onaindia et al., 2015; Peña and Ametzaga-Arregi, 2023). The nomenclature employed in this study was derived from the Common International Classification of Ecosystem Services (CICES V5.2) as delineated in Table 1. For further information pertaining to the selected ES, see Appendix A.

2.4. Sampling design and data analysis for forest attributes

2.4.1. Forest location

The surrounding landscape diversity and slope were calculated using QGIS software (version 3.22.14-Białowieża). The slope (%) was

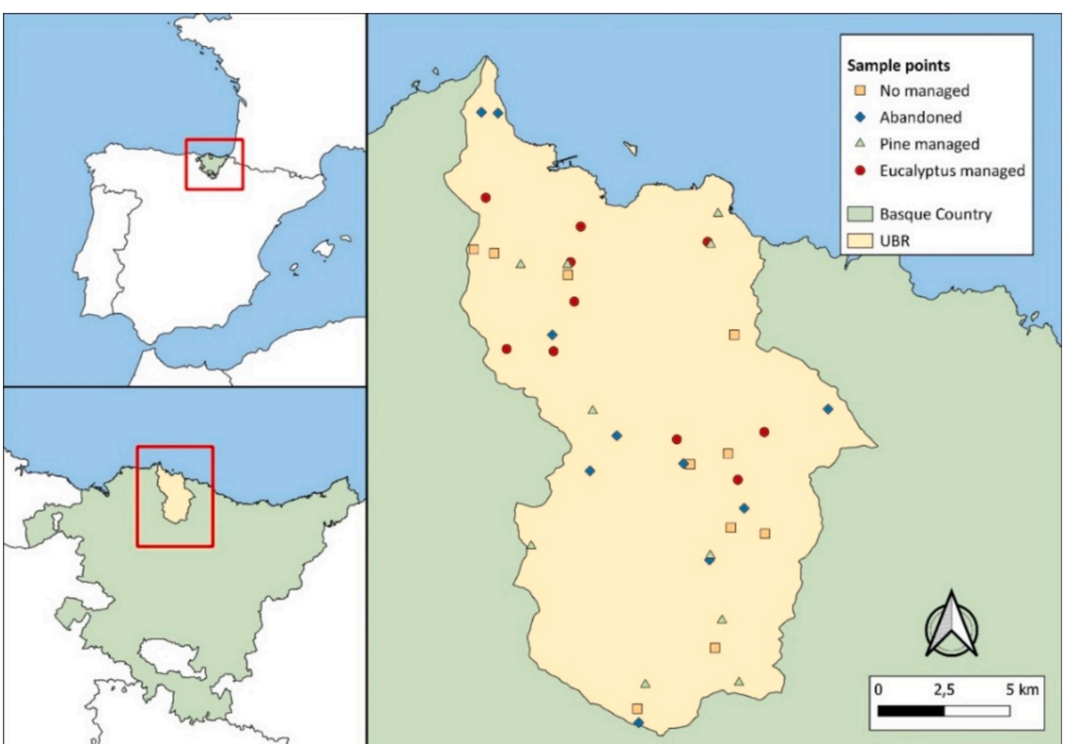

Fig. 1. Location of the sampled stands of each type of forest management in the UBR: No managed (orange squares), Abandoned (blue diamonds), Pine managed (green triangles) and Eucalyptus managed (red circles). The map also highlights the UBR boundary (yellow shade area) within the Basque Country (green area) in Spain. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Summary of the ES evaluated, including their classification by type (categorised into provision, regulation and cultural), the specific service assessed, the indicator used, the method of assessment, and the information required for calculation.

Type	Ecosystem service	CICES V5.2 Code	Indicator	Method	Information used for the calculation
Provision	Food provision: edible fungi	1.1.1.1	Species richness of edible fungi (Felipe-Lucia et al., 2018)	DNA sequencing of soil fungi	Calvo et al., 2016
	Timber provision	1.1.1.2	Extractable Wood Volume (EWV) (m^3 $ha^{-1}yr^{-1}$) (Jullian et al., 2021)	EWV = (Volume (m^3)* Tree density (tree ha^{-1}))/ stand age (year)	Species specific cubing equations (Basque Government, 2005)
Regulation	Habitat maintenance	2.3.2.3 2.3.2.4 2.3.2.5	Plant species diversity (Ampoorter et al., 2020)	Shannon Diversity Index	Plant inventories
	Climate regulation: carbon storage	2.1.1.2	Total carbon content (CT) (tC/ha) (Peña and Ametzaga-Arregi, 2023)	CT = CBv + CBm + Cs CBv = Carbon content in living biomass (tC/ha) CBm = Carbon content in dead biomass (tC/ha) Cs = Soil organic carbon content (tC/ha)	Peña and Ametzaga-Arregi, 2023
	Air quality regulation	2.3.6.1	Canopy cover (%) (Alamgir et al., 2016)	Fisheye canopy photos	
	Water regulation	2.2.2.1 2.2.2.2	Water Retention Index (WRI) (Vandecasteele et al., 2018)	WRI = (WRv Rv + WRgw Rgw + WRs Rs + Wslope Slope) WRv, WRgw, WRs, Wslope = Weights for each factor Rv=Vegetation interception Rgw = Substrate permeability Rs = Soil water retention capacity	Peña and Ametzaga-Arregi, 2023
	Soil erosion control	2.2.1.1 2.2.1.2 2.2.3.1	Vegetation Stratification Index (VSI) (Alamgir et al., 2016)	VSI = $a_tC_T + a_sC_S + a_GC_G + a_lC_L$ a_t, a_s, a_G, a_l = Weights for each factor C_T= Tree cover; C_s = Shrub cover C_G = Grass cover; C_l = Litter cover	Zhongming et al., 2010
	Soil fertility maintenance: nutrient cycling	2.1.1.1 2.3.4.1 2.3.4.2	Species richness of fungi and bacteria related to the nutrient cycling function	DNA sequencing of soil fungi and bacteria	
	Biological control: pest control	2.3.3.1	Insectivorous bird abundance (Dinesh et al., 2022)	Point counts	Bird inventories
	Biological control: soil phytopathogen control	2.3.3.2	Species richness of fungi and bacteria	DNA sequencing of soil fungi and bacteria	
	Regulation of extreme events: wind protection	2.2.3.3	Coefficient of variation of DBH (Alamgir et al., 2016)	Forest structure sampling	
Cultural	Traditional knowledge	3.2.1.3	Medicinal plant species richness	Plant inventories	Menéndez Baceta, 2015
	Recreation: bird-watching potential	3.1.1.2	Bird species richness (Felipe-Lucia et al., 2018)	Point counts	Bird inventories

calculated within a 25-metre radius of each sampling point by a Digital Terrain Model (DTM) using the information from the Harmonised Topographic Base dataset obtained from GeoEuskadi. The surrounding landscape was analysed by categorising land use into six classes: native forests, eucalyptus plantations, pine plantations, open habitats (grasslands, meadows, and shrublands), urban areas, and water bodies. The percentage of area occupied by each land-use within a 250 m buffer zone around the sampling point was determined. The Shannon diversity index was applied to the percentages of each land use in order to quantify landscape diversity.

2.4.2. *Forest structure*

In each selected stand, a random sampling point was selected, and two 50-meter transects were established, one parallel to the slope and the other perpendicular to it (Brower and Zar, 1978). Along each transect, nine subplots (2 m × 5 m) were systematically placed at 5-metre intervals, in which vegetation cover for each species (%) was visually estimated across five strata (0–20 cm (E1), 20–1 m (E2), 1–3 m (E3), 3–7 m (E4), and > 7 m (E5) (Onaindia et al., 2004). The Shannon diversity index was then applied to vegetation covers in order to quantify vertical heterogeneity (Montes et al., 2004).

At three points along the parallel transect (15 m, 30 m, and 45 m), the *Square Centre Point* method (Mostacedo and Fredericksen, 2000; Peña et al., 2011) was used to calculate tree density and mean DBH (m). Tree density was estimated using the following formula: Tree density (tree/ha) = $10000/(ad)^2$, where *ad* is the average distance from the trees to the central reference point (Mostacedo and Fredericksen, 2000). The study involved the measurement of 12 trees in each stand.

2.4.3. *Deadwood*

Along the parallel transect, the diameter of all pieces of deadwood (cm) in contact with the transect line and exceeding 2 cm in diameter was measured. The classification of each piece was undertaken according to the following five decay stages: 1 (recent), 2 (no decay), 3 (slightly decay), 4 (advanced decay), and 5 (very advanced decay) (Özdemir et al., 2023). The total volume of deadwood in early decay stages (1 and 2) and late decay stages (4 and 5) (m^3/ha) was calculated using the following formula (Marshall et al., 2000): Total volume per hectare (m^3/ha) = $(\pi^2/8L)\ \Sigma d^2$, where L is the transect length and d is the diameter of individual pieces of deadwood for each decay stage. Additionally, the Shannon diversity index was applied to the total volume of deadwood across the decay stages to quantify the diversity of decay stages.

2.4.4. *Soil*

In order to obtain a representative sample of the soil, three sampling points were established at random. A composite soil sample was collected at each point, comprising three subsamples taken to a depth of 20 cm. The diameter of the core used for each point was 6.25 cm. The samples were stored in a portable refrigerator at a temperature of 4 °C until they were transported to the laboratory. Initially, the pH was measured using a pH-meter, and subsequently, the samples were dried at room temperature (i.e. 20 °C), sieved using a 2 mm mesh size and stored in darkness for further analysis. The analysis of soil organic matter percentage was conducted in accordance with the standardised protocols established by the Ionomic Service (Research Support Service, CEBAS-CSIC, Murcia, Spain).

2.5. Sampling design and data analysis for ES

2.5.1. Forest structure

The Extractable Wood Volume, which is used as a proxy to assess timber provision, was calculated using previously calculated tree density (tree/ha), volume (m^3) and stand age (yr). Tree volume was estimated from field measurements of tree height and DBH, applying species-specific cubing equations developed for the Basque Country (Basque Government, 2005). Stand age was determined by interpreting high-resolution orthophotos, which allowed us to identify the approximate year of plantation establishment for each stand. The same tree volume estimates were subsequently used to calculate the carbon content in living biomass, which was incorporated into the assessment of carbon storage.

In the three sampling points used for measuring forest structure, canopy cover percentage and Leaf Area Index (LAI) values were calculated from hemispheric canopy photographs taken north-facing and 1.5 m above ground with a mobile phone equipped with a fisheye converter. These values were then analysed with Gap Light Analyzer software (version 2.0; Frazer et al., 1999). The canopy cover was used to evaluate the air quality regulation, while the LAI was employed to assess the vegetation interception, a factor instrumental in calculating the Water Retention Index (Table 1).

Finally, the coefficient of variation of DBH was calculated in order to evaluate wind protection. This index was calculated by dividing the standard deviation of DBH by its mean value for each stand.

2.5.2. Deadwood

For the assessment of carbon storage, the same procedure applied to deadwood attributes was used to estimate the total volume of all deadwood pieces, regardless of decay stage. This total deadwood volume was then used to calculate the carbon content in dead biomass, which was incorporated into the assessment of carbon storage.

2.5.3. Soil

In order to extract the total DNA, 250 mg of soil was sieved from the samples using the DNeasy PowerSoil Pro Kit, in accordance with the manufacturer's instructions. The DNA was shipped to Novogene (Cambridge, UK) for the purpose of PCR amplification for the identification of fungal and bacterial species, using the ITS2 and 16S rRNA V3–V4 regions, respectively (Buée et al., 2009; Christensen et al., 2023). All PCR reactions were carried out with 15 μL of Phusion® High-Fidelity PCR Master Mix (New England Biolabs); 0.2 μM of forward and reverse primers, and approximately 10 ng of template DNA. The identification of species was conducted at a 97 % identity threshold, employing the UNITE and SILVA 138.1 databases (Quast et al., 2013; Abarenkov et al., 2023). A functional annotation was subsequently facilitated through the utilisation of FunGuild (Nguyen et al., 2016) and FAPROTAX (Louca et al., 2016), thereby enabling the elucidation of functional characteristics of each individual fungal and bacterial species. Subsequently, the species richness of edible fungi, fungi and bacteria, and fungi and bacteria related to the nutrient cycling function were calculated to assess the provision of edible fungi, soil phytopathogen control, and nutrient cycling, respectively (Table 1).

Furthermore, soil total carbon percentage was calculated in accordance with the standardised protocols established by the Ionomic Service (Research Support Service, CEBAS-CSIC, Murcia, Spain) to asses carbon storage ES. In order to express this value as carbon stock per unit area (tC/ha), the percentage of carbon was multiplied by the bulk density of each soil sample and the depth of sampling, thereby obtaining the carbon content per hectare of soil.

Finally, previously calculated organic matter percentage and the maximum static storage capacity in topsoil (mm) (URA, 2014) were employed to calculate soil water retention capacity. With regard to the substrate permeability, the soil infiltration capacity (cm/h) and the percolation capacity of the rock stratum (cm/h) were used. Substrate permeability and soil water retention capacity, both are necessary factors to calculate Water Retention Index.

2.5.4. Vegetation

In the nine subplots previously delineated, plant species were visually identified and categorised into three life-form groups (trees, shrubs and herbs) (Aizpuru et al., 1999). The covers (%) of the three groups and the litter cover (%) were determined, in order to calculate the Vegetation Stratification Index (Zhongming et al., 2010) to asses soil erosion control. Moreover, the Shannon diversity index (Shannon and Weaver, 1949) was calculated for all plant species and the medicinal plant species richness to assess habitat maintenance and traditional knowledge, respectively (Table 1). The list of identified plant species is provided in Appendix B (Table B2).

2.5.5. Bird

Bird inventories were conducted using the point count method during the spring season. Surveys were performed at dawn and incorporated auditory and visual observations over a 10-minute period (Proença et al., 2010). This method was employed to ascertain the abundance of insectivorous birds and the bird species richness, which were used to assess pest control and recreation ES (Table 1). The list of identified bird species can be found in Appendix B (Table B21).

2.6. Assessment of the ES supply and the multifunctionality

The selected ES were evaluated using specific proxies based on bibliography. The calculation of these proxies followed the methodology outlined in Table 1 and explained in Section 2.4. A multifunctionality index was subsequently calculated in order to provide an integrated measure of the forest systems' ability to supply multiple ES simultaneously. The calculation of this index entailed the normalisation of the data for each ES indicator, employing the respective maximum and minimum values that had been observed in the dataset. These normalised values were subsequently added together in order to obtain the multifunctionality score (Rodríguez-Loinaz et al., 2015; Manning et al., 2018; Hölting et al., 2019).

2.7. Statistical analysis

Firstly, the normality and homoscedasticity of the ES indicators and the multifunctionality value were verified. In order to compare those variables across the four forest management types, appropriate statistical tests were applied. For variables with a normal distribution, where all were homoscedastic, an analysis of variance (ANOVA) test was conducted, with a Tukey *post-hoc* test. For non-normally distributed variables, the Kruskal-Wallis test was used, with a Dunn test for post-hoc.

Subsequently, Generalised Linear Mixed Models (GLMMs) were employed to identify the forest attributes significantly related to ES supply and multifunctionality. The forest management type was included as a random effect, while forest attributes were treated as explanatory variables. Subsequently, in order to ascertain the absence of multicollinearity among the explanatory variables, a Variance Inflation Factor (VIF) analysis was conducted. This analysis confirmed that all VIF values were below the threshold, thereby indicating the absence of strong correlations. The models were fit using a Gamma distribution for continuous positive response variables and a Poisson distribution for count data. The initial model selection process began with the most complex model, where the least significant variable was systematically removed at each stage. This process was repeated until only variables with significant effects remained. The performance of models was evaluated using the Bayesian Information Criterion (BIC), with models selected as the best fit based on those with the lowest BIC. Moreover, the visualisation of significant relationships within each model was achieved by plotting predicted slopes and their respective confidence intervals. It was observed that forest management type influenced the provision of six ES (timber provision, habitat maintenance, carbon storage, air quality regulation, soil erosion control, and wind protection), as well as the multifunctionality (Appendix C: Fig. C1 and C2).

Finally, to characterise the forest management types based on forest attributes, the four types were compared by applying the statistical tests previously outlined. All statistical tests were performed using R software (v 4.2.2; R Core Team 2020) in R Studio platform (RStudio Team, 2020).

3. Results

3.1. Effect of forest management on ES supply and multifunctionality

All ES indicators exhibited significant differences among the forest management types, with the exception of nutrient cycling (Table 2). In general, the *No managed* stands exhibited a significantly higher ES supply than both the *Eucalyptus managed* and *Pine managed*, in nearly all ES, except for timber provision, where *No managed* had the lowest values, and carbon storage, where *No managed* had significantly lower values compared to *Eucalyptus managed*. Additionally, no significant differences were observed between: i) the *No managed* and *Eucalyptus managed* groups in wind protection, ii) the *No managed* and *Pine managed* groups in carbon storage and phytopathogen control, and iii) the *No managed* and *Abandoned* groups in any ES, with the exception of timber provision and carbon storage, where *Abandoned* demonstrated significantly higher values than *No managed* (Table 2).

For the *Abandoned*, significantly, higher values were observed in comparison to both *Eucalyptus* and *Pine managed,* in almost all ES, except for timber provision and edible fungi provision, where no significant differences were found. Furthermore, no significant differences were detected between *Abandoned* and *Pine managed* for air quality regulation, phytopathogen control, and cultural ES, nor between *Abandoned* and *Eucalyptus managed* for carbon storage, erosion control or phytopathogen control (Table 2).

Finally, *Pine managed* exhibited significantly higher values than *Eucalyptus managed* only for habitat maintenance, phytopathogen control, and traditional knowledge, while *Eucalyptus managed* showed significantly higher values than *Pine managed* only for carbon storage and wind protection (Table 2).

With regard to multifunctionality, *No managed* and *Abandoned* exhibited a significantly higher value than *Pine* and *Eucalyptus managed.* Nevertheless, no significant differences were found between these two types (Table 2 and Fig. 2).

3.2. Forest attributes associated with ES supply and multifunctionality

The results demonstrated a significant correlation between forest attributes and ES provision in all cases, with the exception of air quality regulation and bird-watching potential. The forest attributes that exhibited the strongest correlation with the highest number of ES were soil pH, which demonstrated a significant positive relationship in all models, except for edible fungi provision and water regulation. In contrast, vertical heterogeneity and soil organic matter exhibited a significant positive correlation with these last two ES. Additionally, vertical heterogeneity was found to be positively related to pest control and wind protection, while soil organic matter was linked to traditional knowledge. Finally, the volume of deadwood in late decay showed a significant positive relationship with water regulation and pest control, deadwood decay diversity was positively related to edible fungi provision, and landscape diversity was positively associated with wind protection (Fig. 3).

Conversely, slope, soil organic matter, and the volume of deadwood in early decay exhibited a significant negative correlation with phytopathogen control. Additionally, slope demonstrated a significant negative correlation with carbon storage, habitat maintenance, and erosion control. Furthermore, tree density demonstrated a significant negative correlation with erosion control, and the volume of deadwood in early decay exhibited a negative association with habitat maintenance (Fig. 3).

With regard to the multifunctionality, the results indicated that only three forest attributes demonstrated a significant correlation with it. On the one hand, vertical heterogeneity and pH exhibited a positive correlation with it, while slope demonstrated a negative correlation (Table 3).

3.3. Characterization of types of forest management based on forest attributes

The results indicated significant differences in forest attributes among the four forest management types, with the exception of attributes related to forest location and the volume of deadwood in early decay. The most pronounced differences were exhibited by *Eucalyptus managed*, which were characterised by significantly higher tree density compared to the other management types, while the values for DBH and soil pH were significantly lower. Furthermore, the volume of deadwood in late decay was found to be lower when compared to unmanaged

Table 2
Comparison analysis of the ES supply and multifunctionality value between (mean ± SE) the different types of forest management. Different letters within lines indicates significant differences between types of forest managements.

Ecosystem services		Statistical Test	p-value	Management type			
				No managed	Abandoned	Pine managed	Eucalyptus managed
Provision	Edible fungi provision	Kruskall-Wallis	0.04 *	2.30 ± 0.59 a	1.7 ± 0.36 ab	0.8 ± 0.29 b	0.9 ± 0.34 b
	Timber provision		<0.01*	7.27 ± 1.24 a	31.92 ± 4.39 b	28.83 ± 3.66 b	35.04 ± 6.60 b
Regulating	Carbon storage	Kruskall-Wallis	<0.01*	291.1 ± 66.82 a	882.65 ± 99.31 b	375.69 ± 44.49 a	856.34 ± 135.44 b
	Habitat maintenance	ANOVA	<0.01*	2.58 ± 0.07 a	2.46 ± 0.05 a	1.97 ± 0.05 b	1.57 ± 0.03 c
	Air quality regulation		<0.01 *	74.55 ± 2.53 a	71.24 ± 2.59 ab	63.36 ± 2.61 bc	59.91 ± 1.80 c
	Water regulation		<0.01 *	4.33 ± 0.23 a	4.2 ± 0.25 a	3.2 ± 0.27 b	3.17 ± 0.20 b
	Soil erosion control		<0.01 *	69.9 ± 3.83 a	63.4 ± 4.58 ab	41.97 ± 2.61 c	54.5 ± 2.91 bc
	Nutrient cycling	Kruskall-Wallis	0.48	829.5 ± 117.37	704.53 ± 59.00	771.78 ± 67.43	623.53 ± 49.19
	Pest control	ANOVA	<0.01 *	11.2 ± 0.44 a	10.5 ± 0.58 a	7.2 ± 0.48 b	5.4 ± 0.45 b
	Phytopathogen control	Kruskall-Wallis	0.04 *	1813.9 ± 192.98 a	1626.16 ± 101.89 ab	1807.43 ± 127.67 a	1386.25 ± 62.36 b
	Wind protection	ANOVA	<0.01*	0.43 ± 0.03 ab	0.48 ± 0.05 a	0.18 ± 0.03 c	0.33 ± 0.03 b
Cultural	Traditional knowledge	Kruskall-Wallis	<0.01 *	12.7 ± 0.76 a	11.4 ± 0.74 ab	9.9 ± 0.76 b	6.9 ± 0.48 c
	Bird-watching potential	ANOVA	<0.01 *	6.90 ± 0.60 a	6.80 ± 0.32 ab	5.20 ± 0.41 bc	3.80 ± 0.35 c
Multifunctionality		ANOVA	<0.01*	7.23 ± 0.39 a	7.10 ± 0.41 a	4.36 ± 0.30 b	3.75 ± 0.27 b

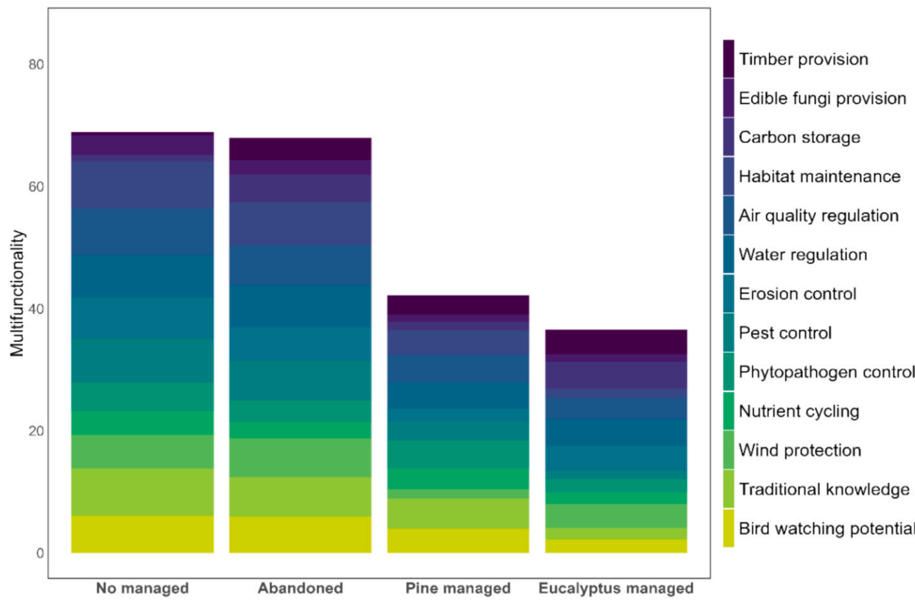

Fig. 2. Contribution of the normalised values of each ES to the multifunctionality value in each type of forest management.

stands (*No managed* and *Abandoned*). Finally, the diversity of decay stages was found to be lower when compared to *Pine managed* and *No managed*. Conversely, *Pine managed* stands exhibited significantly lower vertical heterogeneity in comparison to unmanaged groups, along with a reduced volume of deadwood in late decay compared to *Abandoned* stands. Both *Eucalyptus* and *Pine managed* forests also showed a significantly lower percentage of soil organic matter content compared to unmanaged ones (Table 4). Finally, Pine plantations (both *Abandoned* and *Pine managed*) exhibited the highest DBH values among the forest management types, while *Abandoned* demonstrated the highest volumes of deadwood in late decay (Table 4).

4. Discussion

4.1. Effects of intensive forest management on ES supply and multifunctionality

The results underscore the relevant role of forest management in shaping ES provision (Schwaiger et al., 2019) and multifunctionality, as significant differences were identified across the four distinct forest management types analysed. Forest systems that have remained unmanaged for extended periods (native forests and abandoned pine plantations) exhibited the highest values for most ES supply and multifunctionality (Jullian et al., 2021). In contrast, managed plantations exhibited the highest values solely for timber provision, and the lowest values for multifunctionality, primarily due to the prioritisation of timber provision often coupled with unsustainable practices for the conservation of other ES (Schwaiger et al., 2019; Helseth et al., 2022).

These findings indicate that unmanaged systems generally supply a more extensive range of ES, particularly those services that are of particular importance to human well-being, such as the habitat maintenance and water regulation (Mori et al., 2017; Felipe-Lucia et al., 2018). Similarly, the provision of cultural ES was found to be higher in unmanaged systems. The capacity of forest ecosystems to provide cultural ES depends largely on their complex structure and biological diversity (Himes et al., 2020). This attribute is often lacking in managed plantations, which tend to exhibit structural and compositional simplification (Sutherland, et al., 2016). Consequently, the limited provision of cultural ES in managed plantations underscores the necessity of integrating strategies that enhance the cultural value of forests, particularly in protected areas such as the UBR, where the interaction between nature and local culture is fundamental to the community (Castillo-Eguskitza et al., 2017).

Conversely, the presence of managed plantations has been observed to diminish the capacity of forests to provide ES and multifunctionality. In this context, while managed plantations, particularly eucalyptus plantations, exhibit rapid growth and efficient carbon sequestration, these benefits are undermined by their short lifespan and the rapid release of stored carbon back into the atmosphere (Rodríguez-Loinaz et al., 2013; Castro-Díez et al., 2021). Additionally, aggressive management practices frequently result in substantial nutrient loss through soil erosion, particularly in areas with complex topography, thereby further diminishing the long-term sustainability of these systems (Olarieta et al., 1999). In contrast, native forests exhibit a more gradual accumulation of carbon, yet over extended periods, this storage demonstrates greater stability and attains higher levels in comparison to plantations (Rodríguez-Loinaz et al., 2013; Castro-Díez et al., 2021). Furthermore, eucalyptus plantations demonstrated a reduced capacity to supply key regulating ES, including phytopathogen and pest control, water regulation, soil erosion control, and habitat maintenance. This deficiency is largely attributed to their homogeneous structure, limited quantities of late-decay deadwood, and reduced soil organic matter, which diminish the plantations' resilience to pests and diseases, and restrict the number of microhabitats necessary for biodiversity (Sutherland et al., 2016; Sever and Nagel, 2019; Shimales et al., 2023). The impact of such plantations on soil properties, nutrient availability, and microbial communities is significantly. This is due to the poor-quality litter produced by these plantations and the intensive management practices they undergo, including short rotation cycles and high tree densities (Elosegi et al., 2020; Mallen-Cooper et al., 2022; Castro-Díez et al., 2021). This is evidenced by the fact that the management of forests focusing on specific ES such as timber provision, can inadvertently compromise the supply of other crucial ES (Vadell et al., 2022).

Conversely, due to the longer rotation periods of pine plantations, the differences in ES supply of this management type compared to unmanaged systems were significant but less pronounced, especially for some ES (habitat maintenance and traditional knowledge). Nevertheless, certain ES, including, water regulation, soil erosion control and pest control, exhibited the same reduced capacity as eucalyptus plantations. Additionally, the infestations of red band and brown spot needle diseases that have severely affected pine plantations in recent decades underscore the necessity of considering a broader number of ES beyond

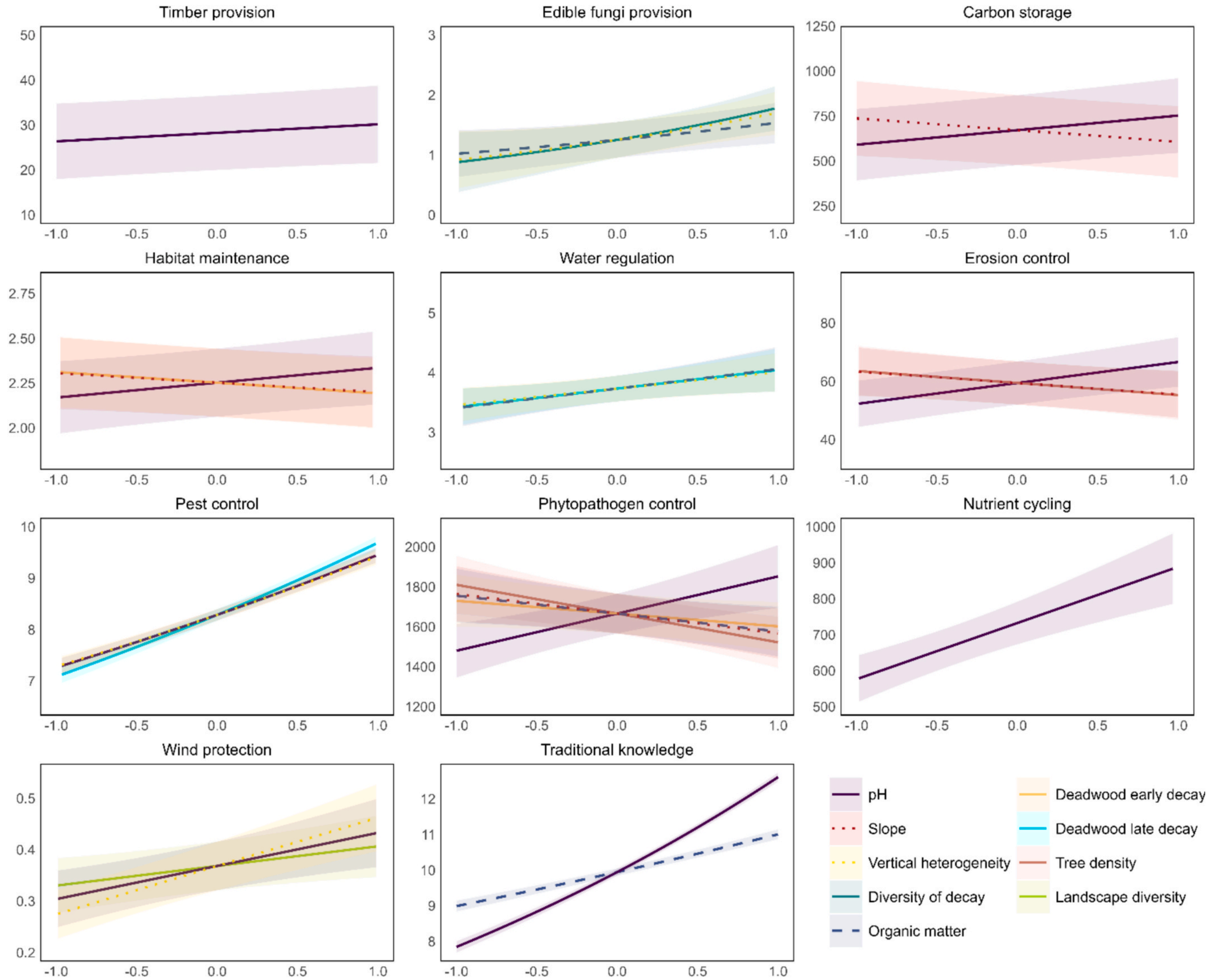

Fig. 3. Predicted slopes of the significant associations derived from the GLMMs between forest attributes and ES. Lines of varying colours and line types are employed to denote the studied forest attributes. The shaded regions represent the 95% confidence intervals.

Table 3
Estimated effects of forest attributes for multifunctionality model. Significance: ***: p ≤ 0.001; **: p ≤ 0.01; *: p ≤ 0.05.

Forest Attribute	Estimate		t value	Pr (<|t|)
Location	Slope	−0.379	−2.530	0.016*
Structure	Vertical heterogeneity	0.493	2.637	0.013*
Soil properties	pH	0.801	5.076	<0.001***

timber provision alone (Ortuño et al., 2022). The effects of these notorious regional mortality events, as evidenced on *Pinus radiata* plantations, have not been incorporated within the experimental framework of this study. Consequently, this may serve to amplify the loss of multifunctionality and ES supply under pine plantations, as evidence by the results obtained in this study.

It is evident from the findings that the natural regeneration of forest attributes, including the recruitment of native tree species, an increase in structural complexity, and the amount of late-decay deadwood and soil organic matter, is facilitated by reduced management intensity in abandoned pine plantations. This, in turn, enhances multifunctionality, as has been observed in other studies linking forest structure and ES provision (Gamfeldt et al., 2013; Amazonas et al., 2018; Felipe-Lucía et al., 2018). It is noteworthy that the abandoned pine plantations exhibited no significant differences in ES supply such as habitat maintenance, pest control, and bird-watching potential when compared with native forests. This finding indicates that, within a comparatively brief timeframe, these abandoned plantations have the potential to attain a level of ecosystem functioning that is analogous to that of native forests. These results are consistent with those reported by Onaindia et al. (2013b), who demonstrated that the return of native species resulting from the abandonment or the management relaxation in the Basque Country promotes the development of structurally diverse habitats, enhancing ecological resilience and enabling the provision of multiple ES. However, it is important to highlight that in pine plantations even when management is abandoned, pine trees remain dominant. This differentiates them from native forests in several ways, including their increased susceptibility to specific pests and diseases (Monteiro et al., 2022; Ortuño et al., 2022). Moreover, it is important to note that some studies have highlighted the potential risk of increased fire hazards associated with unmanaged forests due to the accumulation of combustible material (Wunder et al., 2021). Notwithstanding this concern, the risk of wildfires is comparatively low in the Basque Country, due to its climatic conditions (Trigo et al., 2016, Rodrigues et al., 2020).

Table 4
Comparison of forest attributes across different types of forest management. Different letters within lines indicates significant differences between types of forest management.

Forest attributes		Statistical Test	p-value	Management type			
				No managed	Abandoned	Pine managed	Eucalyptus managed
Location	Slope	ANOVA	0.31	40.45 ± 3.55	31.78 ± 3.48	34.13 ± 3.19	32.58 ± 3.90
	Landscape diversity		0.28	1.26 ± 0.04	1.13 ± 0.06	1.18 ± 0.06	1.24 ± 0.03
	Vertical heterogeneity	Kruskall-Wallis	<0.01**	1.53 ± 0.01 a	1.53 ± 0.01 a	1.40 ± 0.02 b	1.48 ± 0.01 ab
Structure	DBH	ANOVA	<0.01**	0.29 ± 0.02 a	0.45 ± 0.02 b	0.42 ± 0.02 b	0.20 ± 0.01 c
	Tree density	Kruskall-Wallis	<0.01**	872.66 ± 84.83 a	774.41 ± 79.89 a	676.86 ± 110.81 a	2091.1 ± 234.63 b
	Volume of deadwood in early decay	Kruskall-Wallis	0.15	6.90 ± 3.87	8.05 ± 2.66	9.14 ± 2.98	5.47 ± 3.90
Maturity	Volume of deadwood in late decay	Kruskall-wallis	<0.01**	41.79 ± 10.37 ab	55.44 ± 11.74 a	16.84 ± 5.03 bc	1.70 ± 1.23 c
	Diversity of decay stages	Kruskall-Wallis	0.04*	0.90 ± 0.07 a	0.88 ± 0.07 ab	0.97 ± 0.07 a	0.49 ± 0.13 b
Soil properties	Organic matter	Kruskall-Wallis	<0.01**	18.86 ± 1.80 a	17.55 ± 2.66 a	12.40 ± 2.13 b	11.05 ± 0.49 b
	pH	Kruskall-Wallis	0.02*	5.35 ± 0.29 a	5.16 ± 0.30 a	5.30 ± 0.21 a	4.36 ± 0.15 b

4.2. *Drivers associated with ES supply and multifunctionality*

The results indicated that slope, vertical heterogeneity, and soil pH were the forest attributes most significantly associated with multifunctionality, emphasising the critical role of soil pH in supporting a broader range of ES. Specifically, soil pH emerged as a key predictor of regulating ES provision, demonstrating a positive correlation with the majority of those ES. This finding is consistent with the literature, which indicates that a balanced soil pH facilitates nutrient availability and promotes vegetation health, which in turn translates into a greater capacity to ES supply (Fierer and Jackson, 2006; Fornara and Tilman, 2008), including habitat maintenance, erosion control, fertility maintenance and pest and phytopathogen control. In contrast, intensively managed stands frequently exhibit adverse effects on soil health, a consequence of practices such as clear-cutting and soil preparation prior to planting. It has been demonstrated that the implementation of such activities frequently results in the removal of vegetation and the topsoil layer, leading to significant nutrient loss through soil erosion, with losses exceeding 200 $tha^{-1}yr^{-1}$, in some cases (Edeso et al., 1999). Such degradation has been shown to diminish soil quality and reduce its capacity to support ES (Cui et al., 2023). The negative impact is particularly pronounced in areas with steeper slopes, a characteristic of many forest plantations in the Basque Country. Indeed, a negative correlation was observed between slope and four regulating ES including habitat maintenance, carbon storage, erosion control, and phytopathogen control.

Moreover, the implementation of intensive management practices has been demonstrated to exert a significant influence on the vertical structure of forests, resulting in a deficiency in differentiation across vegetation strata that consequentially reduces structural complexity (Onaindia et al., 2013b). Additionally, managed forests typically contain a low volume of deadwood, which is predominantly in early decay stages (Jonsson et al., 2006; Ranius and Roberge, 2011). The aforementioned limitations have been shown to have a detrimental effect on the availability of suitable habitats for a variety of species, including edible fungi. This, in turn, has been demonstrated to result in a reduction in biodiversity and a weakening of the trophic network, a critical component for pest control and overall ecosystem resilience (Schuldt et al., 2018). The consequences of a simplified forest structure and complexity extend further to essential ES, such as water regulation and wind protection. A more complex forest structure and diverse canopy can mitigate the impact of heavy rainfall and strong winds, regulating the amount of water reaching the soil and promoting more efficient water use (Panferov et al., 2010; Helseth et al., 2022, Liu et al., 2023). Similarly, the presence of soil organic matter has been demonstrated to have a significant impact on the enhancement of water-holding capacity, which influences the process of water regulation. At the same time, late-decay deadwood contributes significantly to moisture retention and serves as a habitat for decomposer organisms and other invertebrates. These organisms are vital for the maintenance of habitat, the recycling of nutrients, and the control of pests and phytopathogens (Fornara and Tilman, 2008). Additionally, the positive relationship between wind protection and landscape diversity could be explained by its influence on forest structure complexity, as diverse landscapes may facilitate species input from nearby habitats, increasing the variability in tree sizes (Redon, et al., 2014).

It is evident that management practices, which maintain optimal soil conditions, increase volumes of deadwood at various decay stages, and improve the heterogeneity of forest structure, are essential for fostering multifunctional landscapes and ensuring a high supply of ES. At the same time, the necessity for mixed-species has been identified as a means of ensuring a stable supply of ES (Himes et al., 2020; Vadell et al., 2022). Finally, ES-multifunctionality measures and their relationship to biotic and abiotic drivers have the potential to inform forest management and support environmental decision-making related to landscape management (Manning et al., 2018).

4.3. *Forest management alternatives to improve multifunctionality*

A reduction in the intensity of forest management, coupled with a prioritisation of the conservation of natural forests, is critical for the establishment of resilient, multifunctional landscapes, particularly within protected areas (Azevedo et al., 2014; Mori et al., 2017). Such areas, including Biosphere Reserves, serve as model regions for the exploration of novel techniques and the dissemination of knowledge pertaining to sustainable development. Consequently, managers and policymakers are encouraged to consider the context-specific dependencies of ecosystems and the potential effects of exotic species plantations on a wide range of ES when formulating decisions (Castro-Díez et al., 2021). Specifically, we recommend considering the gradual replacement of eucalyptus plantations with native species in the UBR (Vadell et al., 2022).

Conversely, pine plantations have the capacity to serve as catalysts for the regeneration of native forest species. However, the occurrence of natural regeneration is contingent upon the presence of certain conditions, including the existence of a well-preserved soil seed bank or proximity to native forest stands capable of providing seeds (Amezaga and Onaindia, 1997; Calviño-Cancela et al., 2012). However, conventional management practices in pine plantations frequently impede natural regeneration and increase susceptibility to invasion by alien species, thereby disrupting ecological dynamics and reducing native biodiversity (Sitzia et al., 2018). Addressing these challenges by reducing management intensity or adopting more sustainable practices, especially in Biosphere Reserves, could provide significant benefits for biodiversity conservation and ES supply (Schwaiger et al., 2019).

Consequently, the implementation of “closer-to-nature” management practices could result in a relatively expeditious and favourable impact on the forest’s capacity to provide multiple ES (Felton et al., 2024; Repo et al., 2024). These practices, such as the promotion of the conservation of native forests and the facilitation of the regeneration and recruitment of native species through the relaxation of management in former plantations, are increasingly promoted across Europe (Peura et al., 2018; Caicoya et al., 2023). Their aim is to enhance habitat provision by increasing structural diversity, such as incorporating deadwood, promoting species diversity, and enhancing the growth of mature or large trees. These approaches have been demonstrated to support the production of timber and non-timber resources, as well as biodiversity conservation and non-material benefits (Betts et al., 2021; Larsen et al., 2022).

In contexts such as Biosphere Reserves, where the conservation and sustainable use of natural resources coexist, the implementation of such strategies is essential for fostering a balance between ecological preservation and economic activity. However, it is crucial to align these strategies with the practices and interests of the reserve's stakeholders. Conservation initiatives in protected areas that adopt a top-down approach and disregard local practices or concerns often face resistance and conflict (Hummel et al., 2019). In order to address this issue, establishing collaboration between landowners, forest rangers, scientists and private companies is particularly important. The collective dissemination of knowledge pertaining to species selection, timing, and methodologies for daily management practices enables stakeholders to formulate collaboratively comprehensive and well-informed management strategies that facilitate the harmonious coexistence of biodiversity conservation and sustainable resource utilisation (Zafra-Calvo et al., 2024).

Furthermore, the findings emphasise the significance of incorporating multifunctionality as an integrated indicator of forest ecosystem health and sustainability (Manning et al., 2018; Hölting et al., 2019). This is crucial in forest management, as it provides a comprehensive overview of the sustainability of systems and their responsiveness to environmental change. Comprehending and monitoring multifunctionality is particularly important for facilitating the implementation of management practices that optimise timber provision while also preserving or enhancing regulating and cultural ES. These ES are of equal value to society and the long-term resilience of the ecosystem (Costanza et al., 2017). These findings could be extrapolated to other Biosphere Reserves or regions to promote more sustainable forest management practices, aligning with their primary objectives.

From a policy perspective, these results can inform regional and European strategies aimed at promoting multifunctional and climate-resilient forests. The EU Forest Strategy for 2030, for example, highlights the importance of afforestation and sustainable forest management to restore ES, setting a target of three billion additional trees by 2030. Applying our framework in this context could help identify locally suitable species and management regimes that maintain multifunctionality. At the regional level, our findings are directly relevant to the forthcoming provincial forestry regulation in Bizkaia, which aims to strengthen forest protection, enhance restoration efforts, and improve decentralised monitoring and planning. By identifying key forest attributes such as structural heterogeneity and soil pH as drivers of multifunctionality, this study provides practical evidence that can guide the design of management strategies aligned with these policy objectives.

4.4. Strengths and limitations of the applicability of the framework

The main strength of this framework lies in its adaptability to different regional contexts. As it relies on locally relevant ES, field-based indicators, and comparative assessment among prevailing management types, it can be applied in diverse forested landscapes to support evidence-based policy and management decisions. Beyond the site-specific findings, this study demonstrates the applicability of a field-based, multi-indicator framework for assessing forest multifunctionality. The combination of *in situ* data and indicator-based analysis allows for a more direct quantification of management impacts on ES compared to model- or inventory-based approaches. The use of simple, measurable indicators (e.g., soil pH, vertical heterogeneity, deadwood volume) facilitates replication in other forest contexts, making the framework particularly suitable for regions with limited access to large-scale datasets.

Nevertheless, the approach is data- and labour-intensive, as collecting *in situ* information requires expert participation, time, and financial resources, which may limit its large-scale application. Future implementations could therefore benefit from integrating ground-based data with remote sensing or national forest inventory information to enhance scalability and efficiency.

5. Conclusion

The results of the study demonstrate that intensively managed forest systems, such as pine and eucalyptus plantations, exhibit a diminished capacity to provide ES and multifunctionality, in comparison to unmanaged systems, including Atlantic mixed forests and abandoned pine plantations. This underscores the significance of effective forest management in achieving a balance between the provision of timber and the conservation of other important regulating and cultural ES, which are indispensable for ensuring long-term sustainability. Soil pH and vertical heterogeneity were identified as key attributes in the provision of multiple ES. The positive correlation between vertical heterogeneity and regulating ES, including pest control and water regulation, reinforces the need to maintain a complex forest structure to maximise ecosystem multifunctionality. In addition, the findings indicated that soil pH exhibited a significant predictive capacity, underscoring the pivotal role of management practices in optimising soil health and pH balance. Conversely, steep slopes were found to be associated with reduced multifunctionality, thereby highlighting the importance of soil conservation measures, in mountainous areas.

Moreover, the abandonment of pine plantations presents a valuable opportunity to enhance multifunctionality through natural regeneration, highlighting the significance of reducing management intensity and preserving natural forests for the creation of resilient, multifunctional landscapes. The integration of "close-to-nature" practices, encompassing the extension of rotation periods, the enhancement of structural diversity, and the incorporation of native species, presents a viable strategy for achieving a harmonious balance between timber production and the conservation of biodiversity, as well as ecosystem sustainability. The findings of this study underscore the significance of adopting sustainable forest management practices that preserve stand structural complexity, enhance soil conditions, and incorporate the interests of local stakeholders. Such approaches are essential for achieving multifunctional landscapes that balance ecological preservation with socio-economic development in protected areas such as the UBR.

CRediT authorship contribution statement

Unai Ortega-Barrueta: Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Unai Sertutxa:** Visualization, Formal analysis, Data curation, Conceptualization. **Ibone Ametzaga-Arregi:** Writing – review & editing, Supervision. **Jorge Curiel Yuste:** Writing – review & editing, Funding acquisition. **Raquel Esteban:** Writing – review & editing, Funding acquisition. **Lorena Ruiz de Larrinaga:** Writing – review & editing, Investigation. **Francisco San Miguel-Oti:** Writing – review & editing, Investigation. **Lorena Peña:** Writing – original draft, Methodology, Conceptualization.

Declaration of competing interest

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

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoser.2025.101793.

Data availability

Data will be made available on request.

References

Abarenkov, K., Nilsson, R.H., Larsson, K.H., Taylor, A.F.S., May, T.W., Frøslev, T.G., Pawlowska, J., Lindahl, B., Põldmaa, K., Truong, C., Vu, D., Hosoya, T., Niskanen, T., Piirmann, T., Ivanov, F., Zirk, A., Peterson, M., Cheeke, T.E., Ishigami, Y., Jansson, A.T., Jeppesen, T.S., Kristiansson, E., Mikryukov, V., Miller, J.T., Oono, R., Ossandon, F.J., Paupério, J., Saar, I., Schigel, D., Suija, A., Tedersoo, L., Kõljalg, U., 2023. The UNITE database for molecular identification and taxonomic communication of fungi and other eukaryotes: sequences, taxa and classifications reconsidered. Nucleic Acids Res. 52 (1), 791–797. https://doi.org/10.1093/nar/gkad1039.

Ainz, M.J., 2008. El monocultivo de pino radiata en el País Vasco: origen y claves de permanencia de un sistema de explotación contrario al desarrollo sostenible. Estudios Geográficos 265, 335–356. https://doi.org/10.3989/estgeogr.0426.

Aizpuru, I., Aseginolaza, C., Uribe-Echebarria, P.M., Urrutia, P., Zorrakin, I., 1999. Claves ilustradas de la flora del País Vasco y territorios limítrofes. (Primera edición). Servicio Central de Publicaciones del Gobierno Vasco, Vitoria-Gasteiz.

Alamgir, M., Turton, S.M., Macgregor, C.J., Pert, P.L., 2016. Assessing regulating and provisioning ecosystem services in a contrasting tropical forest landscape. Ecol. Indic. 64, 319–334. https://doi.org/10.1016/j.ecolind.2016.01.016.

Allek, A., Viany Prieto, P., Korys, K.A., Rodrigues, A.F., Latawiec, A.E., Crouzeilles, R., 2023. How does forest restoration affect the recovery of soil quality? A global meta-analysis for tropical and temperate regions. Restor. Ecol. 31 (3), e13747. https://doi.org/10.1111/rec.13747.

Amazonas, N.T., Forrester, D.I., Oliveira, R.S., Brancalion, P.H.S., 2018. Combining Eucalyptus wood production with the recovery of native tree diversity in mixed plantings: Implications for water use and availability. For. Ecol. Manage. 418, 34–40. https://doi.org/10.1016/j.foreco.2017.12.006.

Amezaga, I., Onaindia, M., 1997. The effect of evergreen and deciduous coniferous plantations on the field layer and seed bank of native woodlands. Ecography 20 (3), 308–318. https://doi.org/10.1111/j.1600-0587.1997.tb00375.x.

Azevedo, J., Perera, A.H., Pinto, M.A., 2014. Forest landscapes and global change: challenges for research and management. Springer.

Barraqueta, P., Basagoiti, M., 1988. Acumulación de la hojarasca y aporte de nutrientes en plantaciones de Pinus radiata en el País Vasco. Biología Ambiental: Actas Del Congreso De Biología Ambiental (II Congreso Mundial Vasco) 1, 411–426.

Basque Government, 2004. Plan Rector del Uso y Gestión de la Biosfera de Urdaibai. Departamento de Ordenación Territorial y Medio Ambiente, Vitoria-Gasteiz.

Basque Goverment, 2005. Inventario Forestal CAE 2005.

Betts, M.G., Phalan, B.T., Wolf, C., Baker, S.C., Messier, C., Puettmann, K.J., Green, R., Harris, S.H., Edwards, D.P., Lindenmayer, D.B., Balmford, A., 2021. Producing wood at least cost to biodiversity: integrating Triad and sharing–sparing approaches to inform forest landscape management. Biol. Rev. 96 (4), 1301–1317. https://doi.org/10.1111/brv.12703.

Blattert, C., Lemm, R., Thürig, E., Stadelmann, G., Brändli, U.B., Temperli, C., 2020. Long-term impacts of increased timber harvests on ecosystem services and biodiversity: a scenario study based on national forest inventory data. Ecosyst. Serv. 45, e101150. https://doi.org/10.1016/j.ecoser.2020.101150.

Brockerhoff, E.G., Gresham, B.A., Meurisse, N., Nahrung, H.F., Perret-Gentil, A., Pugh, A.R., Sopow, S.L., Turner, R.M., 2023. Pining away and at home: global utilisation of Pinus radiata by native and non-native insects. NeoBiota 84, 137–167. https://doi.org/10.3897/NEOBIOTA.84.95864.

Brower, J.E., Zar, J.H., 1978. Field and Laboratory Methods for General Ecology. WM. C. Brown Company Publishers, Dubuque, Iowa.

Buée, M., Reich, M., Murat, C., Morin, E., Nilsson, R.H., Uroz, S., Martin, F., 2009. 454 Pyrosequencing analyses of forest soils reveal an unexpectedly high fungal diversity. New Phytol. 184 (2), 449–456. https://doi.org/10.1111/j.1469-8137.2009.03003.x.

Caicoya, A.T., Vergarechea, M., Blattert, C., Klein, J., Eyvindson, K., Burgas, D., Snäll, T., Mönkkönen, M., Astrup, R., Di Fulvio, F., Forsell, N., Hartikainen, M., Uhl, E., Poschenrieder, W., Antón-Fernández, C., 2023. What drives forest multifunctionality in central and northern Europe? Exploring the interplay of management, climate, and policies. Ecosyst. Serv. 64, 101575. https://doi.org/10.1016/j.ecoser.2023.101575.

Calviño-Cancela, M., Rubido-Bará, M., van Etten, E.J., 2012. Do eucalypt plantations provide habitat for native forest biodiversity? For. Ecol. Manage. 270, 153–162. https://doi.org/10.1016/j.foreco.2012.01.019.

Calvo, F.J., Román, J.A., Ibarretxe, R., Calvo, A., 2016. Setas. La guía definitiva. Asociación Micológica Fungipedia, Ediciones Oberon.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., MacE, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486 (7401), 59–67. https://doi.org/10.1038/nature11148.

Carpenter, S.R., Bennett, E.M., Peterson, G.D., 2006. Scenarios for ecosystem services: an overview. Ecol. Soc. 11 (1). https://www.jstor.org/stable/26267787.

Castillo-Eguskitza, N., Rescia, A.J., Onaindia, M., 2017. Urdaibai Biosphere Reserve (Biscay, Spain): conservation against development? Sci. Total Environ. 592, 124–133. https://doi.org/10.1016/j.scitotenv.2017.03.076.

Castro-Díez, P., Alonso, Á., Saldaña-López, A., Granda, E., 2021. Effects of widespread non-native trees on regulating ecosystem services. Sci. Total Environ. 778. https://doi.org/10.1016/j.scitotenv.2021.146141.

Chan, K.M.A., Shaw, M.R., Cameron, D.R., Underwood, E.C., Daily, G.C., 2006. Conservation planning for ecosystem services. PLoS Biol. 4 (11), e379.

Christensen, H., Andersson, J., Jørgensen, S.L., Vogt, J.K., 2023. 16S rRNA amplicon sequencing. introduction to bioinformatics in microbiology. Learn. Mater. Biosci. 153–181. https://doi.org/10.1007/978-3-031-45293-2_8.

Cifuentes-Croquevielle, C., Stanton, D.E., Armesto, J.J., 2020. Soil invertebrate diversity loss and functional changes in temperate forest soils replaced by exotic pine plantations. Sci. Rep. 10 (1). https://doi.org/10.1038/s41598-020-64453-y.

Costanza, R., De Groot, R., Braat, L., Kubiszewski, I., Fioramonti, L., Sutton, P., Farber, S., Grasso, M., 2017. Twenty years of ecosystem services: how far have we come and how far do we still need to go? Ecosyst. Serv. 28, 1–16. https://doi.org/10.1016/j.ecoser.2017.09.008.

Cui, R., Wang, C., Cheng, F., Ma, X., Cheng, X., He, B., Chen, D., 2023. Effects of successive planting of eucalyptus on soil physicochemical properties 1–3 generations after converting Masson pine forests into eucalyptus plantations. Pol. J. Environ. Stud. 32 (5), 4503–4514. https://doi.org/10.15244/pjoes/169015.

Dinesh, G.K., Priyanka, B., Anokhe, A., Ramesh, P.T., Venkitachalam, R., Kerthana Sri, K.S., Abinaya, S., Soni, R., 2022. Ecosystem services and ecological role of birds in insect and pest control. Plant Protection: From Chemicals to Biologicals, pp. 463–504.

Edeso, J.M., Merino, A., González, M.J., Marauri, P., 1999. Soil erosion under different harvesting managements in steep forestlands from northern Spain. Land Degrad. Dev. 10 (1), 79–88. https://doi.org/10.1002/(SICI)1099-145X(199901/02)10:1<79::AID-LDR324>3.0.CO;2-4.

Ehbrecht, M., Seidel, D., Annighöfer, P., Kreft, H., Köhler, M., Zemp, D.C., Puettmann, K., Nilus, R., Babweteera, F., Willim, K., Stiers, M., Soto, D., Boehmer, H.J., Fisichelli, N., Burnett, M., Juday, G., Stephens, S.L., Ammer, C., 2021. Global patterns and climatic controls of forest structural complexity. Nat. Commun. 12 (1), 519. https://doi.org/10.1038/s41467-020-20767-z.

Elosegi, A., Cabido, C., Larrañaga, A., Arizaga, J., 2020. Efectos ambientales de las plantaciones de eucaliptos en Euskadi y la península ibérica. Munibe Ciencias Naturales 68, 111–136. https://doi.org/10.21630/mcn.2020.68.20.

Felton, A., Belyazid, S., Eggers, J., Nordström, E.M., Öhman, K., 2024. Climate change adaptation and mitigation strategies for production forests: Trade-offs, synergies, and uncertainties in biodiversity and ecosystem services delivery in Northern Europe. Ambio 53 (1), 1–16. https://doi.org/10.1007/s13280-023-01909-1.

FAO. 2020. Global Forest Resources Assessment 2020: Main report. Rome. doi:10.4060/ca9825en.

Felipe-Lucia, M.R., Soliveres, S., Penone, C., Manning, P., van der Plas, F., Boch, S., Prati, D., Ammer, C., Schall, P., Gossner, M.M., Bauhus, J., Buscot, F., Blaser, S., Blüthgen, N., de Frutos, A., Ehbrecht, M., Frank, K., Goldmann, K., Hänsel, F., Allan, E., 2018. Multiple forest attributes underpin the supply of multiple ecosystem services. Nat. Commun. 9 (1), 4839. https://doi.org/10.1038/s41467-018-07082-4.

Fornara, D.A., Tilman, D., 2008. Plant functional composition influences rates of soil carbon and nitrogen accumulation. J. Ecol. 96 (2), 314–322. https://doi.org/10.1111/j.1365-2745.2007.01345.x.

Frazer, G.W., Canham, C.D. Lertzman, K.P., 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Copyright © 1999: Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.

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, e1340.
Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1 (2), e1500052. https://doi.org/10.1126/sciadv.1500052.
Helseth, E.V., Vedeld, P., Framstad, E., Gómez-Baggethun, E., 2022. Forest ecosystem services in Norway: trends, condition, and drivers of change (1950–2020). Ecosyst. Serv. 58, e101491. https://doi.org/10.1016/j.ecoser.2022.101491.
Himes, A., Puettmann, K., Muraca, B., 2020. Trade-offs between ecosystem services along gradients of tree species diversity and values. Ecosyst. Serv. 44, 101133.
Hölting, L., Jacobs, S., Felipe-Lucia, M.R., Maes, J., Norström, A.V., Plieninger, T., Cord, A.F., 2019. Measuring ecosystem multifunctionality across scales. Environ. Res. Lett. 14 (12), e124083. https://doi.org/10.1088/1748-9326/ab5ccb.
Hoogar, R., Malakannavar, S., Sujatha, H.T., 2019. Impact of eucalyptus plantations on ground water and soil ecosystem in dry regions. J. Pharmacogn. Phytochem. 8 (4), 2929–2933.
Hummel, C., Poursanidis, D., Orenstein, D., Elliott, M., Adamescu, M.C., Cazacu, C., Ziv, G., Chrysoulakis, N., van der Meer, J., Hummel, H., 2019. Protected Area management: fusion and confusion with the ecosystem services approach. Sci. Total Environ. 651, 2432–2443. https://doi.org/10.1016/j.scitotenv.2018.10.033.
Jactel, H., Brockerhoff, E.G., 2007. Tree diversity reduces herbivory by forest insects. Ecol. Lett. 10 (9), 835–848. https://doi.org/10.1111/j.1461-0248.2007.01073.x.
Jonsson, M., Ranius, T., Ekvall, H., Bostedt, G., Dahlberg, A., Ehnström, B., Nordén, B., Stokland, J.N., 2006. Cost-effectiveness of silvicultural measures to increase substrate availability for red-listed wood-living organisms in Norway spruce forests. Biol. Conserv. 127 (4), 443–462. https://doi.org/10.1016/j.biocon.2005.09.004.
Juerges, N., Arts, B., Masiero, M., Hoogstra-Klein, M., Borges, J.G., Brodrechtova, Y., Brukas, V., Canadas, M.J., Carvalho, P.O., Corradini, G., Corrigan, E., Felton, A., Karahalil, U., Karakoc, U., Krott, M., van Laar, J., Lodin, I., Lundholm, A., Makrickienė, E., Marques, M., Mendes, A., Mozgeris, G., Novais, A., Pettenella, D., Pivoriūnas, N., Sarı, B., 2021. Power analysis as a tool to analyse trade-offs between ecosystem services in forest management: a case study from nine European countries. Ecosyst. Serv. 49, e101290, 10.1016/j.ecoser.2021.101290.
Jullian, C., Nahuelhual, L., Laterra, P., 2021. The Ecosystem Service Provision Index as a generic indicator of ecosystem service supply for monitoring conservation targets. Ecol. Ind. 129, e107855. https://doi.org/10.1016/j.ecolind.2021.107855.
Larsen, J.B., Angelstam, P., Bauhus, J., Carvalho, J.F., Diaci, J., Dobrowolska, D., Gazda, A., Gustafsson, L., Krumm, F., Knoke, T., Konczal, A., Kuuluvainen, T., Mason, B., Motta, R., Pötzelsberger, E., Rigling, A., Schuck, A., 2022. Closer-to-Nature Forest Management. From Science to Policy 12. European Forest Institute. doi:10.36333/fs12.
Liu, Y., Shi, W., Tao, F., Shi, X., Fu, B., 2023. A global synthesis of multi-factors affecting water storage capacity in forest canopy, litter and soil layers. Geophys. Res. Lett. 50 (3). https://doi.org/10.1029/2022GL099888.
Loidi, J., Biurrun, I., Campos, J.A., García-Mijangos, I., Herrera, M., 2011. La vegetación de la Comunidad Autónoma del País Vasco. Leyenda del mapa de series de vegetación a escala 1:50.000. Ed. Universidad del País Vasco (edición electrónica).
Louca, S., Parfrey, L.W., Doebeli, M., 2016. Decoupling function and taxonomy in the global ocean microbiome. Science 353 (6305), 1272–1277 https:/doi.org/10.1126/science.aaf4507.
Mallen-Cooper, M., Atkinson, J., Xirocostas, Z.A., Wijas, B., Chiarenza, G.M., Dadzie, F. A., Eldridge, D.J., 2022. Global synthesis reveals strong multifaceted effects of eucalypts on soils. Glob. Ecol. Biogeogr. 31 (8), 1667–1678. https://doi.org/10.1111/geb.13522.
Manning, P., van der Plas, F., Soliveres, S., Allan, E., Maestre, F.T., Mace, G., Whittingham, M.J., Fischer, M., 2018. Redefining ecosystem multifunctionality. Nat. Ecol. Evol. 2 (3), 427–436. https://doi.org/10.1038/s41559-017-0461-7.
Marshall, P.L., Davis, G., LeMay, V.M., 2000. Using Line Intersect Sampling for Coarse Woody Debris. (Technical Report TR-003). Research Section, Vancouver Forest Region, British Columbia Ministry of Forests.
McGrath, M.J., Luyssaert, S., Meyfroidt, P., Kaplan, J.O., Bürgi, M., Chen, Y., Erb, K., Gimmi, U., McInerney, D., Naudts, K., Otto, J., Pasztor, F., Ryder, J., Schelhaas, M.J., Valade, A., 2015. Reconstructing European forest management from 1600 to 2010. Biogeosciences 12 (14), 4291–4316. https://doi.org/10.5194/bg-12-4291-2015.
Menéndez Baceta, G., 2015. Etnobotánica de las plantas silvestres comestibles y medicinales en cuatro comarcas de Araba y Bizkaia. Universidad Autónoma de Madrid.
Monteiro, P., Gonçalves, M.F.M., Pinto, G., Silva, B., Martín-García, J., Diez, J.J., Alves, A., 2022. Three novel species of fungi associated with pine species showing needle blight-like disease symptoms. Eur. J. Plant Pathol. 162, 183–202. https://doi.org/10.1007/s10658-021-02395-5.
Montes, F., Cañellas, I., del Río, M., Calama, R., Montero, G., 2004. The effects of thinning on the structural diversity of coppice forests. Ann. For. Sci. 61 (8), 771–779. https://doi.org/10.1051/forest:2004074.
Mori, A.S., Lertzman, K.P., Gustafsson, L., 2017. Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. J. Appl. Ecol. 54 (1), 12–27. https://doi.org/10.1111/1365-2664.12669.
Mostacedo, B., Fredericksen, T.S., 2000. Manual de Métodos Básicos de Muestreo y Análisis en Ecología Vegetal. Bolfor, Santa Cruz, Bolivia.
Nguyen, N.H., Song, Z., Bates, S.T., Branco, S., Tedersoo, L., Menke, J., Schilling, J.S., Kennedy, P.G., 2016. FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. Fungal Ecol. 20, 241–248. https://doi.org/10.1016/j.funeco.2015.06.006.
Olarieta, J.R., Besga, G., Rodrıguez, R., Uson, A., Pinto, M., Virgel, S., 1999. Sediment enrichment ratios after mechanical site preparation for *Pinus radiata* plantation in the Basque Country. Geoderma 93 (3–4), 255–267. https://doi.org/10.1016/S0016-7061(99)00063-4.
Onaindia, M., Ametzaga-Arregi, I., San Sebastián, M., Mitxelena, A., Rodriguez-Loinaz, G., Peña, L., Alday, J.G., 2013a. Can understorey native woodland plant species regenerate under exotic pine plantations using natural succession? For. Ecol. Manage. 308, 136–144. https://doi.org/10.1016/j.foreco.2013.07.046.
Onaindia, M., Dominguez, I., Albizu, I., Garbisu, C., Amezaga, I., 2004. Vegetation diversity and vertical structure as indicators of forest disturbance. For. Ecol. Manage. 195 (3), 341–354. https://doi.org/10.1016/j.foreco.2004.02.059.
Onaindia, M., Fernández de Manuel, B., Madariaga, I., Rodríguez-Loinaz, G., 2013b. Co-benefits and trade-offs between biodiversity, carbon storage and water flow regulation. For. Ecol. Manage. 289, 1–9. https://doi.org/10.1016/j.foreco.2012.10.010.
Onaindia, M., Madariaga, I., Palacios, I., Arana, X., 2015. Nature and Human Well-being in Biscay. Ecosystem Services Assessment; research applied to management. University of the Basque Country (UPV/EHU), Leioa, Spain, p. 130.
Onaindia, M., Peña, L., Amezaga, I., Rodríguez-Loinaz, G., 2010. Evaluación y localización de los servicios de los ecosistemas en la Reserva de Biosfera de Urdaibai-País Vasco. Servicios Ambientales En Reservas De La Biosfera Españolas 91–106.
Ortega, U., Ametzaga-Arregi, I., Sertutxa, U., Peña, L., 2023. Identifying a green infrastructure to prioritise areas for restoration to enhance the landscape connectivity and the provision of ecosystem services. Landsc. Ecol. 38 (12), 3751–3765. https://doi.org/10.1007/s10980-023-01789-6.
Ortuño, S., González, V., Tolosana, E., 2022. Problemática de las plantaciones de pino radiata en Euskadi: bases de la propuesta de un fondo forestal profesionalizado. 8°Congreso Forestal Español.
Özdemir, S., Yavuz, M., Kahriman, A., 2023. Variation of deadwood density by decay class in pure and mixed oriental spruce stands in Northeastern Black Sea. Eur. J. For. Res. 142 (6), 1453–1466. https://doi.org/10.1007/s10342-023-01601-9.
Panferov, O., Sogachev, A., Ahrends, B., 2010. changes of forest stands vulnerability to future wind damage resulting from different management methods. Open Geogr. J. 3 (1), 80–90. https://doi.org/10.2174/1874923201003010080.
Pedroli, G.B.M., Meiner, A., 2017. Landscapes in transition: an account of 25 years of land cover change in Europe. Eur. Environ. Agency (EEA). https://doi.org/10.2800/81075.
Peña, L., Ametzaga-Arregi, I., 2023. Guía metodológica para el cartografiado de los Servicios de los Ecosistemas en Euskadi.Evaluación de los Servicios de los Ecosistemas de Euskadi. Servicio Editorial de la. Universidad del País Vasco-Euskal Herriko Unibertsitateko Argitalpen Zerbitzua.
Peña, L., Amezaga, I., Onaindia, M., 2011. At which spatial scale are plant species composition and diversity affected in beech forests? Ann. For. Sci. 68, 1351–1362. https://doi.org/10.1007/s13595-011-0147-2.
Peura, M., Burgas, D., Eyvindson, K., Repo, A., Mönkkönen, M., 2018. Continuous cover forestry is a cost-efficient tool to increase multifunctionality of boreal production forests in Fennoscandia. Biol. Conserv. 217, 104–112. https://doi.org/10.1016/j.biocon.2017.10.018.
Peura, M., Triviño, M., Mazziotta, A., Podkopaev, D., Juutinen, A., Mönkkönen, M., 2016. Managing boreal forests for the simultaneous production of collectable goods and timber revenues. Silva Fenn. 50 (5). https://doi.org/10.14214/sf.1672.
Proença, V.M., Pereira, H.M., Guilherme, J., Vicente, L., 2010. Plant and bird diversity in natural forests and in native and exotic plantations in NW Portugal. Acta Oecol. 36 (2), 219–226. https://doi.org/10.1016/j.actao.2010.01.002.
Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., Glöckner, F.O., 2013. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. Nucleic Acids Res. 41 (1), 590–596. https://doi.org/10.1093/nar/gks1219.
Ranius, T., Roberge, J.M., 2011. Effects of intensified forestry on the landscape-scale extinction risk of dead wood dependent species. Biodivers. Conserv. 20 (13), 2867–2882. https://doi.org/10.1007/s10531-011-0143-8.
Redon, M., Bergès, L., Cordonnier, T., Luque, S., 2014. Effects of increasing landscape heterogeneity on local plant species richness: how much is enough? Landsc. Ecol. 29 (5), 773–787. https://doi.org/10.1007/s10980-014-0027-x.
Repo, A., Albrich, K., Jantunen, A., Aalto, J., Lehtonen, I., Honkaniemi, J., 2024. Contrasting forest management strategies: Impacts on biodiversity and ecosystem services under changing climate and disturbance regimes. J. Environ. Manage. 371, e123124. https://doi.org/10.1016/j.jenvman.2024.123124.
Riffo-Donoso, V., Osorio, F., Fontúrbel, F.E., 2021. Habitat disturbance alters species richness, composition, and turnover of the bryophyte community in a temperate rainforest. For. Ecol. Manage. 496, e119467. https://doi.org/10.1016/j.foreco.2021.119467.
Rodrigues, M., Trigo, R.M., Vega-García, C., Cardil, A., 2020. Identifying large fire weather typologies in the Iberian Peninsula. Agric. For. Meteorol. 280, e107789. https://doi.org/10.1016/j.agrformet.2019.107789.
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. https://doi.org/10.1016/j.jenvman.2014.09.001.
Rodríguez-Loinaz, G., Amezaga, I., Onaindia, M., 2013. Use of native species to improve carbon sequestration and contribute towards solving the environmental problems of the timberlands in Biscay, northern Spain. J. Environ. Manage. 120, 18–26. https://doi.org/10.1016/j.jenvman.2013.01.032.
Schuldt, A., Assmann, T., Brezzi, M., Buscot, F., Eichenberg, D., Gutknecht, J., Härdtle, W., He, J.S., Klein, A.M., Kühn, P., Liu, X., Ma, K., Niklaus, P.A., Pietsch, K. A., Purahong, W., Scherer-Lorenzen, M., Schmid, B., Scholten, T., Staab, M., Tang, Z., Trogisch, S., von Oheimb, G., Wirth, C., Wubet, T., Zhu, C.D., Bruelheide, H., 2018. Biodiversity across trophic levels drives multifunctionality in highly diverse forests. Nat. Commun. 9 (1), e2989. https://doi.org/10.1038/s41467-018-05421-z.

Schwaiger, F., Poschenrieder, W., Biber, P., Pretzsch, H., 2019. Ecosystem service trade-offs for adaptive forest management. Ecosyst. Serv. 39, e100993. https://doi.org/10.1016/j.ecoser.2019.100993.
Sertutxa, U., Ortega-Barrueta, U., Ametzaga-Arregi, I., Peña, L., 2024. Effect of the rotation frequency in the eucalypt plantations. For. Ecosyst. 11, e100251. https://doi.org/10.1016/j.fecs.2024.100251.
Sever, K., Nagel, T.A., 2019. Patterns of tree microhabitats across a gradient of managed to old-growth conditions. Acta Silvae et Ligni 118, 29–40. https://doi.org/10.20315/asetl.118.3.
Shannon, C.E., Weaver, W., 1949. The Mathematical Theory of Communication. University of Illinois Press, Urbana.
Shimales, T., Mendesil, E., Zewdie, B., Ayalew, B., Hylander, K., Tack, A.J.M., 2023. Management intensity affects insect pests and natural pest control on Arabica coffee in its native range. J. Appl. Ecol. 60 (5), 911–922. https://doi.org/10.1111/1365-2664.14410.
Sitzia, T., Campagnaro, T., Kotze, D.J., Nardi, S., Ertani, A., 2018. The invasion of abandoned fields by a major alien tree filters understory plant traits in novel forest ecosystems. Sci. Rep. 8 (1), e8410.
Spielvogel, S., Prietzel, J., Auerswald, K., Kögel-Knabner, I., 2009. Site-specific spatial patterns of soil organic carbon stocks in different landscape units of a high-elevation forest including a site with forest dieback. Geoderma 152, 218–230.
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. Ind. 71, 123–133. https://doi.org/10.1016/j.ecolind.2016.06.037.
Trigo, R.M., Sousa, P.M., Pereira, M.G., Rasilla, D., Gouveia, C.M., 2016. Modelling wildfire activity in Iberia with different atmospheric circulation weather types. Int. J. Climatol. 36 (7), 2761–2778. https://doi.org/10.1002/joc.3749.
Turner, J., Lambert, M.J., Hopmans, P., Mcgrath, J., 2001. Site variation in Pinus radiata plantations and implications for site specific management. In New Forests 21, 249–282. https://doi.org/10.1023/A:1012240720833.
URA, 2014. Actualización de la evaluación de recursos hídricos de la CAPV 2010.
Vadell, E., Pemán, J., Verkerk, P.J., Erdozain, M., de-Miguel, S., 2022. Forest management practices in Spain: understanding past trends to better face future challenges. For. Ecol. Manage. 524, e120526. https://doi.org/10.1016/j.foreco.2022.120526.
Vandecasteele, I., Marí i Rivero, I., Baranzelli, C., Becker, W., Dreoni, I., Lavalle, C., Batelaan, O., 2018. The Water Retention Index: using land use planning to manage water resources in Europe. Sustain. Dev. 26 (2), 122–131. https://doi.org/10.1002/sd.1723.
Vaz, A.S., Honrado, J.P., Lomba, A., 2019. Replacement of pine by eucalypt plantations: effects on the diversity and structure of tree assemblages under land abandonment and implications for landscape management. Landsc. Urban Plan. 185, 61–67. https://doi.org/10.1016/j.landurbplan.2019.01.009.
Winkel, G., Lovrić, M., Muys, B., Katila, P., Lundhede, T., Pecurul, M., Pettenella, D., Pipart, N., Plieninger, T., Prokofieva, I., Parra, C., Pülzl, H., Roitsch, D., Roux, J.L., Thorsen, B.-J., Tyrväinen, L., Torralba, M., Vacik, H., Weiss, G., Wunder, S., 2022. Governing Europe's forests for multiple ecosystem services: opportunities, challenges, and policy options. Forest Policy Econ. 145, e102849. https://doi.org/10.1016/j.forpol.2022.102849.
Wunder, S., Calkin, D.E., Charlton, V., Feder, S., de Arano, I.M., Moore, P., Rodríguez y Silva, F., Tacconi, L., Vega-García, C., 2021. Resilient landscapes to prevent catastrophic forest fires: socioeconomic insights towards a new paradigm. Forest Policy Econ. 128, 102458. https://doi.org/10.1016/j.forpol.2021.102458.
Zafra-Calvo, N., Ortega, U., Sertutxa, U., Moreaux, C., 2024. Identifying key actors, barriers and opportunities to lead a transition towards sustainable forest management: an application to the Basque Country, Spain. Trees, Forests and People 18, e100727. https://doi.org/10.1016/j.tfp.2024.100727.
Zhongming, W., Lees, B.G., Feng, J., Wanning, L., Haijing, S., 2010. Stratified vegetation cover index: a new way to assess vegetation impact on soil erosion. Catena 83 (1), 87–93. https://doi.org/10.1016/j.catena.2010.07.006.