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## Biodiversity conservation effectiveness provided by a protection status in temperate forest commons of north Spain

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**Abstract:** The establishment and maintenance of protected areas is the backbone of global conservation strategies to halt biodiversity loss. However, despite the more than 200,000 legally designated protected sites worldwide, the rate of species extinction has not decreased, for which some debate the real effectiveness of protected areas to preserve biodiversity. Using data from tropical areas, many studies have attempted to test the effectiveness of protected areas by comparing species richness in protected and neighbouring unprotected sites, without reaching a consensus. Here, we extend this line of research with data from temperate deciduous forests inside and outside Picos de Europa National Park and Biosphere Reserve (N Spain). Specifically we compare data from mixed broadleaved woodlands, beech forests (*Fagus sylvatica* L.) and Pyrenean oak (*Quercus pyrenaica* Willd.) forests. We conducted botanical inventories and recorded ecological data from 25 0.2-ha concentric plots distributed in forest commons inside the reserve and from other 25 similar plots established in neighbouring not protected forest commons. Data were used to construct a set of ecological indicators and evaluated using modelling methods. We found no significant differences in species composition between plots in protected and non-protected forest commons, likely due to the similar management criteria applied in both land uses. We found less active management outside the protected area, which helps to maintain stands in a semi-natural state. In contrast, we observed the presence of silvicultural treatments inside the protected area, although these treatments were non-intensive, promoting vegetation composition associated to late-successional ecosystems. We only detected significant differences between plots inside and outside the protected area when relation between species richness was analysed

with reference to forest habitat type. Precisely, plots of beech forests inside Picos de Europa were more homogenous than plots outside the protected area, which may indicate that management practices inside the protected area do not favour tree species diversity. Non-intensive silviculture management in beech forests inside Picos de Europa seems to promote the presence of the dominant tree species *Fagus sylvatica* L., which in the absence of perturbations is characterized by conforming monospecific vegetation communities. Overall, our results do not support the idea that protected areas hold more biodiversity than surrounding forest commons. Conservation treatments applied in protected areas should promote the presence of species associated to disturbances, particularly in stands tending to homogeneous species composition at late-successional stages, as this may enhance their resilience under the current rapid global changes.

**Keywords:** Anthropogenic disturbances; biodiversity indices; protected area; species richness; temperate deciduous forests.

## 1. Introduction

With 234,468 Protected areas (PA) already established worldwide (IUCN, UNEP-WCMC, 2017), site designation rate is considered one of the most remarkable conservation successes of the twentieth century (Gaston et al., 2008). If this trend continues, the goal of 17% coverage for terrestrial and inland waters by 2020 under Aichi Biodiversity Target 11 would be achieved (Gannon et al., 2017). However, in numerous cases, site designation has followed an exclusionary approach –referred to as ‘neo-protectionist’ or ‘fortress conservation’ approach (Wilshusen et al., 2002; Brockington, 2002)– resulting in the displacement and dispossession of communities residing in the newly protected site, and often led to contested actions (Laudati, 2010; Mahapatra et al., 2015). Moreover, even when less controversial ‘conservation-centric’ initiatives have been applied to the establishment of a PA, such as protected sites created in partnership with local people, conflicts with local residents have still arisen, especially when the establishment of a PA have prevented local users from the management of the surrounding natural resources (West et al., 2006). As the economic basis of many indigenous peoples and local communities is closely dependant on the goods obtained from neighbouring natural areas, particularly forests (Angelsen et al., 2014), when restrictions to local use are applied without providing suitable alternative livelihood options, struggles are likely to appear (Mahapatra et al., 2015), constituting a significant shortcoming to PA conservation efforts (Andrade and Rhodes, 2012).

There is evidence of better biodiversity conservation outcomes from PA management strategies integrating local economic activities than from strictly conservation PA management regimes (Oldekop et al., 2016), for which many conservationists nowadays embrace a more integrative perspective for the establishment and management of PA (Shultis and Heffer, 2016). Notions such as social-ecological systems, resilience, or cultural landscape are holistic approaches which

consider people as part of their surrounding environment rather than mere passive users of landscape biophysical components. People modify their living and adjacent territories, sometimes causing the depletion of natural resources, but sometimes coevolving with nature in the benefit of a sustainable use and promotion of a dynamic mosaic of ecosystems at the landscape level. Along these lines, scholars increasingly advocate for considering PAs as 'social-ecological systems' (Hirschnitz-Garbers and Stoll-Kleemann, 2011; Cumming et al., 2015; Mathevet et al., 2016), a conceptual framework that contemplates both the social and ecological aspects of the system as equally important (Berkes, 2017). Under the social-ecological systems approach, the social and the natural systems are indeed coupled subsystems that co-evolve, which implies that societies are able to adapt to perturbations in the environment and vice versa. Given the rapid global changes occurring nowadays, the co-evolving capacity offered by the social-ecological systems approach brings to light the idea that societies have the opportunity to face environmental challenges without compromising long-term sustainability of ecosystems (Berkes et al., 2003).

The growing scholarly emphasis on conservation efforts outside the physical boundaries of PAs focuses on reconcile management practices from land uses, such as farming or forestry, with biodiversity conservation (Kremen, 2015). Research on practices that may be both favourable to biodiversity and economically profitable has significantly increased attention to the potential that community-based resource management may bring to foster a sustainable use of ecological resources (Xu and Melick, 2007; Larson et al., 2016). Through practices such as clearing, livestock grazing, or swidden agriculture, humans have modified landscapes for millennia, partially replacing the ecological functions that megaherbivores used to play in shaping vegetation structures of terrestrial biomes (Sandom et al. 2014; Bocherens, 2018). While not all of these small and intermediate-scale disturbances have a positive effect in preserving biodiversity, overall, management practices applied by communities seem to enhance biodiversity through the creation of a mosaic of ecosystems (Agrawal and Gibson, 1999; Guèze et al., 2015).

Aiming to further understand the conservation outcomes that may result from community resource management, here we study a community-based regime that can be considered a social-ecological systems: forest commons. Forest commons are characterized by having clearly defined boundaries and legal enforceable property rights and by providing resources to a variety of social groups that are usually involved in their management (Aryeetey et al., 2012). The importance of forest resources to support rural household economies strongly engaged local communities in the monitoring of their surrounding woodlands to prevent mismanagement and overexploitation, resulting in the implementation of management techniques that allowed the co-existence and long-term maintenance of diverse forest uses and habitats (Parrotta and Troster, 2012; Kirby and Watkins, 2015). Nowadays, forests commons constitute 18% of global forest area and appear to contribute significantly to biodiversity conservation (Chhatre and Agrawal, 2008).

In this work, we analyse the role of forest commons in long-term biodiversity persistence and the effectiveness of protected areas in this type of community-based regime. We do so by comparing a set of ecological and anthropogenic features observed in forest commons plots inside and

outside a PA classified as an IUCN category II (National Park), a very restrictive protection category with regard to human activities (Gray et al., 2016; Hewitt et al., 2016). Our study has three main goals. First, we test whether plots inside and outside the PA differ in their ecological characteristics (i.e. topography, edaphic factors), and how this relates to species richness. We based our null hypothesis on the general assumption that we will find the same tree species abundance and evenness in plots inside and outside the PA. The second goal of this research is to analyse the effect of the human intervention on species distribution in plots under protected and unprotected sites, an analysis performed by linking the variables measuring human disturbances (i.e. plot isolation, silvicultural systems) with tree species occurrence. Based on previous case studies highlighting the association of anthropogenic disturbance with species richness in human-dominated landscape (Guèze et al., 2015; Mod et al., 2016), our hypothesis is that anthropogenic disturbances can induce changes in species composition that would result in more heterogeneous species assemblages of the studied forest communities. Finally, the third goal of this paper is to study the relationship between tree species composition, and particularly species diversity, and a) spatial distribution and b) forest management approach. For this goal we compare three different forest habitat types occurring inside and outside the study PA, in an attempt to quantify the conservation outcomes resulting from the protection status between habitats of the same land use type, i.e. temperate deciduous forests.

## **2. Methods**

### *2.1 Study site*

We conducted the study in the *Liébana* valley (57,500 ha), a wide depression located in the southwest of the Cantabria region, in northern Spain. High elevation differences characterize the region, with altitude ranges from 330 m to 2600 m above sea level. *Liébana* is surrounded by hills, a geographical feature that results in relative geographical isolation with the neighbouring areas and a high number of habitat types of unique ecological value. The bottom of the valley presents a Mediterranean microclimate with less rainfall than the rest of the Cantabria region; at higher altitudes we find an Atlantic climate (Rescia et al., 2008). *Liébana*'s mean temperature varies from 7.9 to 20.8 C and the annual average rainfall varies from 700 to 1500 mm in the mountainous parts (ETSIM, 1978). Topographic and climatic differences result in a very heterogeneous landscape with a wide array of vegetation types.

From a land tenure perspective, common property is a key feature in the *Liébana* region, with almost 80% of its territory under this regime (Arbeo, 2012). More than three quarters of the woodlands in *Liébana* are forest commons (Ministerio de Medio Ambiente, 1997–2007). The area has a long tradition of human intervention, as reflected in the large number of local ordinances regulating forest uses since the 15<sup>th</sup> century (Pérez-Bustamante and Baró, 1988). Management activities have shaped the structure of the local ecosystems and their species composition, at the same time that they have allowed the persistence of high valuable habitats, to the point that 60%

of Liébana's forest commons are currently under some category of protection, including the *Picos de Europa* National Park (hereafter Picos de Europa) in the northwest of the region.

Picos de Europa was the first Park designated in Spain, in 1918, following the North American conservationist model that advocated for the preservation of wilderness areas by preventing human interventions. It also applied a State-led management (Hirschnitz-Garbers and Stoll-Kleemann, 2011; González, 2015). Since its designation, conflicts with local communities in Liébana's neighbouring region arose due to the limitations that the protection status enforced on local uses (e.g., hunting, wood extraction) (Voth, 2007). Conflicts have shaped the negative perception of Liébana's rural communities regarding the extension of Picos de Europa National Park in 1995, which included three municipalities of Liébana, conforming the second largest site of the Spanish National Parks and notably including human settlements within its boundaries. Although the management criteria established in 1995 aimed at making compatible local traditional uses –like livestock herding or fuelwood collection– with biodiversity conservation (Royal Decree No. 640/1994 of Spanish Government), confrontation with local population, particularly livestock farmers, resulted in the revoke of the National Park management plan in 2005 due to a legal action taken by local communities within Picos de Europa buffer zone (Spanish Government, 2005).

The lack of a valid management plan, specific to the area, difficults the regulation of traditional uses. However, and despite the lack of a specific plan, several conservation initiatives are being undertaken inside the national park in response to national and regional environmental legislation, including the recovery plans for the endangered species brown bear (*Ursus arctos*) and Cantabrian capercaillie (*Tetrao urogallus cantabricus*) conservation. Altogether, this situation makes of Picos de Europa a very suitable site to analyse the effects of human activities and conservation management strategies on species diversity.

## 2.2 Description of the forest communities studied

To test the ecological differences between stands inside and outside the PA, we studied the ecological features of the three more abundant habitats in the forest commons inside Picos de Europa, which are also present outside the PA: 1) Mixed broadleaf woodlands, defined as forest with a variable mixture of at least two native broadleaf species accounting for  $\geq 70\%$  of the plot forest cover; 2) Beech forests or forest with *Fagus sylvatica* L. as the dominant tree species, accounting for  $\geq 70\%$  of the plot forest cover; and 3) Pyrenean oak forests, or forest with *Quercus pyrenaica* Willd. as the dominant tree species accounting for  $\geq 70\%$  of the plot forest cover.

### 2.2.1 Mixed broadleaf woodlands

Mixtures of broadleaf species cover most of the territory. Despite some human influence, mixed broadleaf woodlands are considered naturally distributed particularly in areas of contact between

different tree formations. The predominant species in the mixed broadleaf woodlands located in upper altitudes of Liébana are *Quercus pyrenaica*, *Fagus sylvatica*, *Ilex aquifolium* L., and *Crataegus monogyna* Jacq. At lower altitudes, the predominant tree species are conformed by *Castanea sativa* Miller, *Fraxinus excelsior* L., *Tilia cordata* L., *Tilia platyphyllos* Scop., *Quercus ilex* L., and *Corylus avellana* L. (ETSIM, 1978).

### 2.2.2 Beech forests (*Fagus sylvatica* L.)

Forests of *Fagus sylvatica* are the predominant tree species formation in the Liébana valley and, generally, also the ones with the best conservation status and regeneration rates. These woodlands are shade-tolerant and occupy lands from 600 m to 1700 m in shadow slopes, and from 700 to 1300 m in sunny slopes. Beech woods form close, dense stands, where only shade-tolerant species can grow and where the competing tree species need to take advantage of clearings resulting from felling, browsing animals, or fires. As a result, *F. sylvatica* only appears in combination with other species in boundary areas with other forest types, or in areas where it displaces other species, as in the case of *Quercus pyrenaica*. A sparse understorey could accompany beech forests, composed by *Ilex aquifolium*, *Crataegus monogyna*, *Sorbus aria* L. Crantz, and *Corylus avellana*. However, most frequently, the accompanying species are *Pteridium aquilinum* (L.) Kuhn in Kerst and *Rubus* sp., partly due to the increased light following human interventions such as clear cuts (ETSIM, 1978; Godefroid et al., 2005; Kelemen et al., 2012).

### 2.2.3 Pyrenean oak (*Quercus pyrenaica* Willd.)

Forests of *Quercus pyrenaica* occur widely in the Liébana valley, with the species also occurring as a shrub in combination with *Corylus avellana*, *Crataegus monogyna*, *Erica* and *Ulex* sp. in mixed broadleaf woodlands. *Q. pyrenaica* is tolerant to a wide range of site conditions, occurring from 400 to 1300 m in altitude on sunny slopes and from 300 to 1200 on shady ones. Despite its frequency as shrub strata, it appears most often as a tree when the forest is cleared, i.e. when human intervention is high (Tárrega et al., 2006), accompanied by *Corylus avellana*, *Crataegus monogyna*, *Erica arborea* L., *Daboecia cantabrica* (Hunds) C. Koch and *Rubus* sp. Occasionally, it also appears in combination with *Prunus spinosa* L., *Erica vagans* L., *Calluna vulgaris* L. Hull, leguminous species like *Ulex europaeus* L., *Genista florida* L., *Cytisus* sp., or *Quercus ilex* (ETSIM, 1978).

## 2.3 Local history of forest commons management

As mentioned, the area has a long tradition of forest commons management. The invasion of Germanic tribes into the Iberian Peninsula in the fifth century brought the concept of woodlands

collective property to the northwest areas of the peninsula, where forest natural resources were used by local communities (Aranda, 1996). Some centuries later, during the Christian Reconquest (eighth to fifteenth century), the communal regime spread to other parts of the peninsula as a strategy followed by medieval kings to promote the settlement of Christian populations that would displace Muslims from the newly gained territories. Within this process, the crown, ultimate owner of the common lands, granted land concessions –including woodlands– to the new settlers, who organized in village councils or *concejos* to collectively manage and use natural resources (Behar, 1983; Pardo and Gil, 2005).

Forest commons, or *montes comunales* in Spanish, were the most common type of tenure regime in Spanish woodlands until the nineteenth century, when Europe's transition to capitalism gave rise to the establishment of a new liberal framework that initiated a process of privatisation of communal resources. Despite the long tradition of forest commons in Spain, the liberal framework did not recognize communal ownership and just distinguished between the public and private proprietorship of lands and goods. Under that political context, forest commons were classified as public properties and their management transferred to Spanish State Forest Administration (Beltrán, 2015; Guadilla-Sáez et al., 2017). In the Liébana region, forest commons belong to municipalities, while their use corresponds exclusively to local communities, with the regional forestry administration exerting its influence by monitoring access to grazing, firewood, and other forest goods (Balboa, 1999; Pérez-Soba and Solá, 2004). Remarkably, some forest-related stewardship customs still persist today in the study area, such as the neighbourhood councils or *juntas vecinales*, minor local bodies which have replaced former village councils and have legal rights to regulate the use of forest commons (Law No. 6/1994 of Cantabrian Regional Government). As a result, the regional forestry administration management intervention needs the approval from the neighbourhood councils before being applied in forest commons. However, and despite the regional legal enforcement of these minor local bodies role in the management of their common lands, the Picos de Europa Board of Trustees or *Patronato* –i.e. the participatory body aimed to integrate society to management activities and to promote further implications of local residents (Law No. 30/2014 of Spanish Government)–, does not include neighbourhood councils representatives.

#### 2.4 Data collection

We used a GIS procedure to randomly select plots in forest patches with, at least, 70% of tree canopy cover according to the Third Spanish National Forest Inventory (Ministerio de Medio Ambiente, 1997–2007). In each forest type, we located the centre of the plots according to a systematic sampling design in the intersection of a 125 × 125 m fishnet grid created with ArcGIS version 10.3.1 (ESRI, 2015). From the total possible labels, we selected 50 values using the 'randbetween' option of MS Excel and stored their spatial coordinates in a global positioning system (GPS) device. These values were taken as the centre of each plot. We inventoried 50 circular plots of 25 m radius (0.2 ha). Half of the plots were in forest commons inside Picos de

Europa (Fig.1, white-shaded area) and the other half were in forest commons located outside Picos de Europa and not affected by any other formal category of protection (Fig.1, grey-shaded area).

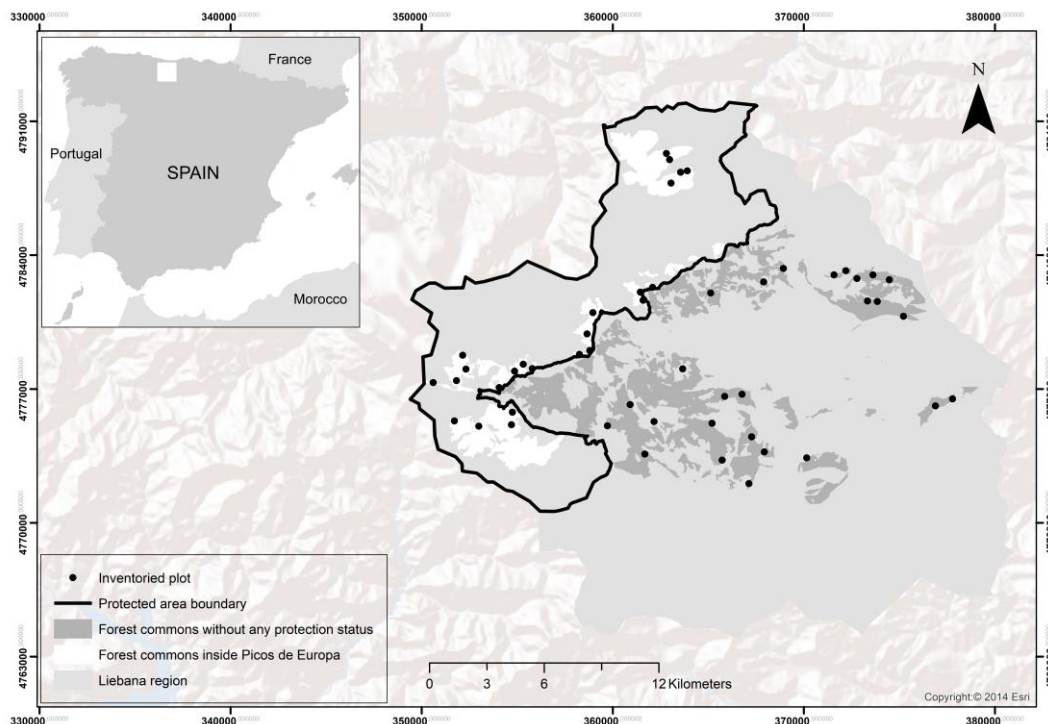


Fig.1. Map of the study area, illustrating the location of the 50 plots across the Liébana region (Cantabria, Spain).

We collected data during 2015 and 2016. We recorded a set of ecological parameters in each of the plots that included their general characteristics, the dominant tree species of the stand, stand structure properties, and distribution of the ground vegetation cover (see appendix B). We inventoried the dendrometric characteristics of the 10 adult trees closest to the centre of the plot, where an adult tree were defined as a tree with more than 3 meters height or with a minimum diameter at breast height (1.30 m) of 7.5 cm. To determine the abundance of each tree species, we identified all tree stems rooted within a sub-plot of 15 meters radius (aprox. 700 m<sup>2</sup> in area). We also quantified the topographic variable slope for every plot using a SUUNTO clinometer and collected a surface soil sample to later analyse pH and texture parameters in the laboratory by using a glass electrode in a suspension of 1:10 soil:distilled water. As additional monitored field measurements, we inventoried other edaphic variables such as soil texture, organic matter thickness, and stoniness. We also recorded the presence of silvicultural treatments such as clear cuttings, brush removal, thinning, or ground improvements within 25 m radius (0.2 ha).

We measured several anthropogenic variables associated with plot disturbance, including plot accessibility and linear distance from the plot centre to the nearest village and nearest path (i.e. unpaved roads or trails), calculated in desktop using ArcGIS version 10.3.1 (ESRI, 2015) in high



resolution aerial photographs derived from the Spanish Aerial Orthophoto National Plan (PNOA, 2015). We also measured population density of the nearest towns using data from the Spanish National Statistics Institute (INE, 2018).

## 2.5 Ecological indices

Species presence indicators are frequently used to monitor effectiveness of a particular forest management treatment in biodiversity conservation (Canadian Council of Forest Ministers, 1997). For this research, we calculated a set of tree species composition indices to examine the heterogeneity in the composition of the studied communities, including the Shannon index ( $H'$ ), a separate measure of evenness ( $J'$ ) from the standardization of the Shannon index, Species Richness ( $D_{Mn}$ ), the complement of the Simpson index ( $1 - D$ ), and the reciprocal form of the Berger-Parker index ( $1/d$ ) (Table 1).

Although most studies have focused on the numerical richness to compare tree species diversity between different ecosystems (Hui et al., 2011), surrogate measures, such as stand structure indicators, are increasingly being used to provide a measure of biodiversity in forest communities (Pommerening, 2002). Following this trend, in this study, we have considered the Clark and Evans Index of aggregation ( $R$ ) to define the distance between neighbouring trees in a forest spatial structure unit (Neumann and Starlinger, 2001). We have also included the Uniform angle (contagion) index ( $W_i$ ), which tests the regularity of the distribution pattern of the trees, and the species complement for the Mingling index ( $1 - M_i$ ) to test the heterogeneity of species among nearest neighbouring trees (Aguirre et al., 2003; Pommerening, 2002). The spatial unit considered for the estimation of the stand structure indices was the group size of the four nearest neighbouring trees to the reference tree, which is considered the optimum group size for evaluating spatial attributes (Hui et al., 2011).

Table 1. List of the diversity and stand structure indices used to analyse the ecological data.		
Index	Formula	Definition
<b>Species composition indices</b>		
Shannon (Magurran, 2004)	$H' = - \sum p_i \ln p_i$	where $p_i$ is the proportion of individuals found in the $i$ species referred to the total number of individuals.
Evenness (Elliott et al., 1997)	$J' = \frac{H'}{H_{max}} = \frac{H'}{\ln S}$	where $H_{max}$ is the maximum level of diversity possible within a given population and $S$ is the total number of species.
Richness (Magurran, 2004)	$D_{Mn} = \frac{S}{\sqrt{N}}$	where $S$ equals the number of different species represented in the sample, and $N$ is the total number of individuals in the sample.

Simpson (Magurran, 2004)	$D = \sum p_i^2$	where $p_i$ is the proportion of individuals in the $i$ th species.
Berger-Parker (Magurran, 2004)	$d = \frac{N_{max}}{N}$	where $N_{max}$ is the number of individuals of the most abundant species and $N$ refers to the total number of individuals.
<b>Stand structure indices</b>		
Clark-Evans (Vorčák et al., 2006)	$R = \frac{\frac{1}{n} \sum_i^n r_i}{0.5 \times \sqrt{\frac{Pl}{n}}}$	where $r_i$ is the distance from the reference tree to its nearest neighbour, $n$ is the number of trees on the sample plot and $Pl$ the area of the sample plot in square meters.
Uniform angle (contagion) index (Pommerening, 2002)	$W_i = \frac{1}{n} \sum_{j=1}^n w_{ij}$	where $w_{ij}$ is 1 if the angle with the $j$ th neighbouring tree is lower than the defined standard angle, and $w_{ij}$ equals 0 otherwise. $n$ is the number of trees on the sample plot.
Species Mingling (Hui et al., 2011)	$M_i = \frac{1}{n} \sum_{j=1}^n v_{ij}$	where $v_{ij}$ is 1 if the $j$ th neighbouring tree is not the same species as the $i$ th reference tree, and $v_{ij}$ equals 0 otherwise. $n$ is the number of trees on the sample plot.

## 2.6 Statistical analyses

### 2.6.1 Indices computed

We estimated tree species presence and stand structure indicators for each forest habitat type and subjected the resulting data to the Shapiro-Wilk normality test (Table A.1). We used a two-sample t-test for testing for differences between forest habitat types inside and outside Picos de Europa for the normally distributed data and a two sample Wilcoxon rank-sum (Mann-Whitney) test for the non-normally distributed data (Table A.2 to Table A.4). Significance levels ( $p$ -values) were adjusted to the number of tests carried out using a standard Bonferroni correction (Zuur et al., 2007). To facilitate the graphical comparison between stands of the three different forest habitats inside and outside the PA, we standardized correlation coefficients, representing in a common scale values obtained. We did all analysis using the STATA software version 13.1 (StataCorp, 2013).

### 2.6.2 Model selection

We considered two explanatory environmental variables in our model: (1) plot topography and (2) soil characteristics. Due to their relevance for the research, we also included as explanatory variables the level of human intervention observed in the plots, including variables that measure

(3) plot isolation –i.e. distance to human infrastructures–, and (4) presence of anthropogenic disturbances –i.e. forest management practices–.

As dependent variable, we used the abundance of individuals per tree species estimated by the Shannon index ( $H'$ ), a simple formula widely used to measure species richness in which the higher the value of  $H'$ , the greater the species diversity of the studied system (Elliot et al., 1997; Magurran, 2004; Zuur et al., 2007). We evaluated the relative importance of the variables that measure environmental characteristics, plot isolation, and anthropogenic disturbances in explaining tree species distribution by using a Wald test analysis of  $H'$  against different models combining the explanatory variables. To select the explanatory variables to be included in the final model, we checked the normality of the variables through a correlation matrix and applying the Shapiro-Wilk normality test (see Table A.5). Based on those results, we selected non-parametric statistics for several of the explanatory variables. To determine relations between the explanatory variables, we applied Pearson's correlation test for the normally distributed variables and Spearman rank correlation test for the variables not-normally distributed (Table A.6). For categorical variables, we used a Pearson's chi-squared correlation. After running the regressions, we removed multiple variables due to collinearity, identified by tolerances values approaching 0.1 in these predictors.

The first step for the model selection consisted in fitting the global models of each set of explanatory variables to the data, examining the goodness-of-fit of each model with a  $\chi^2$  statistical test (Johnson and Omland, 2004). Due to our reduced sample (50 plots), models only included up to four variables at a time, as recommended by Harrell et al. (1996), representing all possible combinations of the variables (excluding interactions) with no model including more than one variable from each general category of variables (i.e. plot topography, soil characteristics, plot isolation, and anthropogenic disturbances). In total, we analysed a total of 479 models. We fit each model to the data by using an Ordinary least squares method and performed model comparison of all possible models by using the Akaike information criterion (AIC) for selecting the best set of explanatory variables in describing the variation of species diversity based on the minimum AIC score (Burnham and Anderson, 2002; Quinn and Keough, 2002; Johnson and Omland, 2004). We calculated the AIC difference ( $\Delta AIC_i$ ) and Akaike weights ( $w_i$ ) for the ten best ranked models fitting the data to assess the statistical level of support for a given model (Table A.7). Due to the low AIC differences between models, we considered a subset of models with  $\Delta AIC_i < 4$  to estimate the relative importance of individual explanatory variables (Burnham and Anderson, 2002). We then repeated the analysis using Richness index as dependent variable.

### **3. Results**

#### *3.1 Protection status and ecological and human disturbance variables*

A one-way ANOVA analysis of variance test showed significant differences in the explanatory and dependent variables measured in forest commons inside and outside Picos de Europa (Table 2).

Mean values of longitude and latitude showed significant difference in plots inside (mean  $\pm$  SD: 368965.8  $\pm$ 5080.0) and outside (357567.4  $\pm$ 4456.5) Picos de Europa, arguably because of the geographical location of the PA in the northwest part of the Liébana region. Our results suggest that there is a significantly thicker layer of organic matter in the soils of the plots outside (7.1  $\pm$ 2.5) than in the soils of plots inside the PA (4.8  $\pm$ 2.8). Additionally, there is a lower presence of surface stones in the plots outside the PA.

Regarding the anthropogenic variables, plots inside Picos de Europa were more distant to towns (2225.6  $\pm$ 907.6) than plots outside the PA (817.2  $\pm$ 434.1), likely due to the reduced number of villages that have their municipality boundaries inside the protected area. Nearest town population density presented an average of 66.6 and 37.6 inhabitants, respectively, a situation explained by the presence of two very touristic villages inside Picos de Europa, *Espinama* and *Pido*. We also found significant differences in the implementation of silvicultural practices, with presence of some type of silvicultural systems –regeneration felling, forest cover improvement and/or ground improvements– in 80% of studied plots inside the PA and only in 52% for plots outside it. Specifically, plots inside Picos de Europa had a higher presence of cover improvement treatments (80%) than plots outside (48%). We did not detect significant differences in the presence of regeneration felling or ground improvement practices.

The census of the 50 sample plots led to the identification of a total of 14 families and 17 tree species, with an average number of 2.52 (SD = 1.7) and 3.8 (SD = 1.5) species per plot in plots inside and outside Picos de Europa, respectively. We observed significant differences between species abundance distributions in Shannon index means across plots. Specifically, the mean Shannon index was lower in plots inside Picos de Europa (0.45  $\pm$ 0.5) than in plots outside it (0.86  $\pm$ 0.4). We did not find significant differences for the Richness index, which also showed lower values in plots inside (0.32  $\pm$ 0.2) than outside Picos de Europa (0.47  $\pm$ 0.3).

Table 2. Mean and standard deviation (SD) (or percentage for categorical variables) of variables considered, by location in relation to Picos de Europa. The One-way ANOVA analysis of variance compares the means in plots outside and inside the protected area, in bold significant differences based on their *p-values* (\*\* *p-value*  $\leq$  0.01; \* *p-value*  $\leq$  0.05).

Variable	Code	Specification	Pool		N <sup>a</sup>	Outside		Inside	
			Mean ( $\pm$ SD)	p-value		Mean ( $\pm$ SD)	N	Mean ( $\pm$ SD)	
<b>Explanatory variable</b>									
<i>Topography</i>									
Longitude	UTMY	Degrees	363266.6 ( $\pm$ 7450.6)	.000	25	<b>368965.8**</b> ( $\pm$ 5080.0)	25	<b>357567.4**</b> ( $\pm$ 4456.5)	
Latitude	UTMX	Degrees	4779509 ( $\pm$ 4620.2)	.042	25	<b>4778188*</b> ( $\pm$ 4004.1)	25	<b>4780830*</b> ( $\pm$ 4890.2)	
Slope	SLO	Percentage	46.9 ( $\pm$ 12.7)	.276	24	48.9 ( $\pm$ 12.5)	25	44.9 ( $\pm$ 12.9)	
<i>Soil characteristics</i>									

pH	PH	Numeric scale	6.2 ( $\pm 0.8$ )	.177	24	6.0 ( $\pm 0.7$ )	21	6.4 ( $\pm 0.95$ )
Texture	TEX	1- Sandy	45.8%	.388	23	43.5%	25	48.0%
		2- Loam	22.9%			39.1%		8.0%
		3- Clay	31.2%			17.4%		44.0%
Organic matter	OM	Centimetres	6.0 ( $\pm 2.9$ )	.004	25	<b>7.1**</b> ( $\pm 2.5$ )	25	<b>4.8**</b> ( $\pm 2.8$ )
Stoniness	STO	1- Without stones	26.0%	.043	25	<b>36.0%*</b>	25	<b>16.0%*</b>
		2- Low stony	32.0%			<b>36.0%*</b>		<b>28.0%*</b>
		3- Stony	18.0%			<b>12.0%*</b>		<b>24.0%*</b>
		4- Very stony	24.0%			<b>16.0%*</b>		<b>32.0%*</b>
<i>Isolation</i>								
Distance to path	DIST1	Meters	161.78 ( $\pm 188.4$ )	.651	25	149.6 ( $\pm 154.1$ )	25	174 ( $\pm 220.1$ )
Distance to town	DIST2	Meters	1521.4 ( $\pm 1000.9$ )	.000	25	<b>817.2**</b> ( $\pm 434.1$ )	25	<b>2225.6**</b> ( $\pm 907.6$ )
Town population	POP	Number of inhabitants	52.7 ( $\pm 31.7$ )	.001	23	<b>37.6**</b> ( $\pm 30.6$ )	25	<b>66.6**</b> ( $\pm 26.3$ )
<i>Anthropogenic disturbances</i>								
Grazing	GRA	0- No presence	32.0%	.071	25	44.0%	25	20.0%
		1- Presence	68.0%			56.0%		80.0%
Silvicultural treatments	SILV	0- No presence	34.0%	.037	25	<b>48.0%*</b>	25	<b>20.0%*</b>
		1- Presence	66.0%			<b>52.0%*</b>		<b>80.0%*</b>
Regeneration felling	FEL	0- No presence	48.0%	.093	25	60.0%	25	36.0%
		1- Presence	52.0%			40.0%		64.0%
Cover improvement	COV	0- No presence	36.0%	.018	25	<b>52.0%*</b>	25	<b>20.0%*</b>
		1- Presence	64.0%			<b>48.0%*</b>		<b>80.0%*</b>
Ground improvement	GRO	0- No presence	96.0%	1.00	25	96.0%	25	96.0%
		1- Presence	4.0%			4.0%		4.0%
<b>Dependent variable</b>								
<b>Shannon</b>	$H'$		0.64 ( $\pm 0.5$ )	.004	21	<b>0.86**</b> ( $\pm 0.4$ )	25	<b>0.45**</b> ( $\pm 0.5$ )
<b>Richness</b>	$D_{Mn}$		0.39 ( $\pm 0.3$ )	.064	21	0.47 ( $\pm 0.3$ )	25	0.32 ( $\pm 0.2$ )

<sup>a</sup> Not available or unclear observations excluded from the analysis.

### 3.2 Ecological indices

Although we observed higher species diversity in the mixed broadleaf woodlands plots inside Picos de Europa than in the plots outside, we did not find any significant differences in the ecological indices calculated (Fig.2 and Table A.2). In contrast, although protected and unprotected *Fagus sylvatica* plots were relatively similar in terms of spatial diversity, the richness and evenness was higher in plots outside (Fig.2 and Table A.3). Finally, we do not find any

significant differences between *Quercus pyrenaica* plots inside and outside the protected area (Fig.2 and Table A.4).

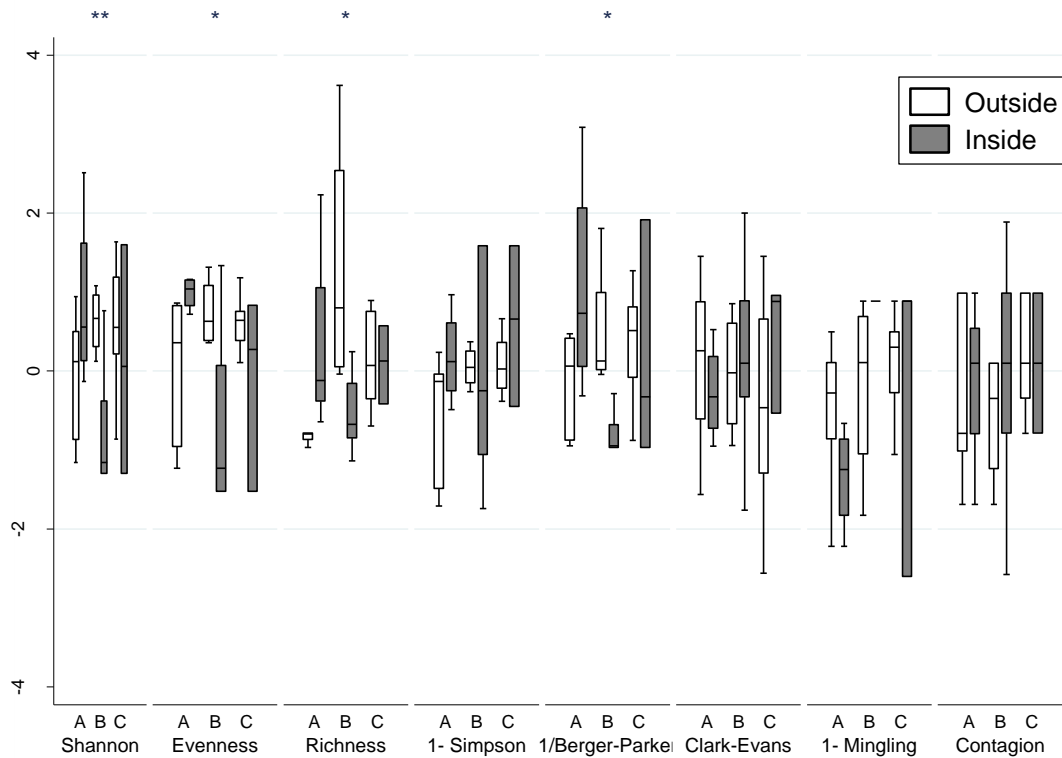


Fig. 2. Boxplots illustrating Z scores for the five species composition indicators (n=46) and the three stand structure ones (n=49) for mixed broadleaf woodlands (A), *Fagus sylvatica* forests (B), and *Quercus pyrenaica* stands (C). Asterisks indicate significant differences in means between protected and unprotected *Fagus sylvatica* forests based on their p-values after Bonferroni correction (\*\* p-value ≤ 0.005; \* p-value ≤ 0.025).

### 3.3 Model selection

According to the AIC, the best-ranked model for explaining the evenness of tree species of forest commons in the Liébana valley is given by Eq. 1:

$$H' = (-0.002) \times SLO + (-0.003) \times PH + (-0.0002) \times DIST2 + (-0.196) \times FEL + 1.287 \quad (1)$$

where  $H'$  is the Shannon index value of the studied plots. This model had an  $AIC_c$  on 47.75 which gave  $w_i = 5.71\%$  (Table A.7). The best-ranked model for explaining the species richness of forest commons in the Liébana valley is given by Eq. 2:

$$D_{Mn} = 0.028 \times OM + (-0.0004) \times DIST1 + 0.289 \quad (2)$$

where  $D_{Mn}$  is the Richness index value for the studied plots. This model had an  $AIC_c$  on 5.22 which gave  $w_i = 2.33\%$  (Table A.7). In both models Akaike weights have a very low value, indicating uncertainty that these models are the best approximating models to our data (Symonds

and Moussalli, 2011). Given this uncertainty, and following McCracken et al. (2015), we tested the dependent variables against the explanatory variables included in the subset of models with  $\Delta AIC_i < 4$ , estimating the Akaike weights for these candidate explanatory variables and their relative importance across the subset models (Table 3).

Table 3. Importance of environmental and anthropogenic variables considered across the 50 study plots. Importance was derived using Akaike weights ( $w_i$ ), reporting in bold the most important variables (with importance $\geq 0.4$ ). See table 2 for variables definition.															
	Topography			Soil characteristics				Isolation			Disturbances				
Variable	UTMY	UTMX	SLO	PH	TEX	OM	STO	DIST1	DIST2	POP	GRA	SILV	FEL	COV	GRO
Response = Shannon index. Models where $\Delta AIC < 4 = 44$ of 473.															
Importance	.05	.06	<b>.63</b>	<b>.44</b>	.29	.04	.08		<b>1</b>		.08	.10	.32	.09	.08
Response = Richness index. Models where $\Delta AIC < 4 = 93$ of 473.															
Importance	.18	.17	.20			<b>.78</b>	.13	<b>.40</b>	<b>.49</b>	.02	.07	.11	.16	.12	.17

The analysis shows that the two abiotic variables slope of the plot (SLO) and soil acidity (PH), as well as the anthropogenic variable distance to nearest town (DIST2) are the explanatory variables most associated with tree species evenness. All these variables bear a negative association with the Shannon index thus suggesting that, in general, species evenness is higher in plots with lower slopes, less acid soils, and closest to human settlements. Presence of anthropogenic disturbances as regeneration felling practices (FEL) also show a negative association to species evenness, although the strength of this association is weak.

In addition, the soil characteristic thickness of organic matter (OM) and the anthropogenic variables distance to nearest path (DIST1) and town (DIST2) seem to play an important role in the distribution of vegetation communities. Tree species richness was positively associated to organic matter thickness, indicating that many species prefer soils with a deep organic humus layer. In contrast, the Richness index was negatively associated to plot isolation variables, showing more species diversity in more accessible plots, or plots located closer to human settlements.

#### 4. Discussion

Our results generally suggest that tree species composition is less heterogeneous inside than outside the Picos de Europa National Park. Two main factors may explain this result: the dominance of monospecific *Fagus sylvatica* forest inside the protected area and the application of silvicultural systems oriented to promote the presence of beech forests inside the protected area. Our results also suggest that human intervention variables, particularly distance to nearest town, are more important drivers of tree species distribution and diversity in forest commons of the Liébana valley than the abiotic factors considered for the analysis.

#### 4.1 Ecological variables

The main goals of this work were to quantify differences in ecological characteristics between forest commons inside and outside Picos de Europa and to analyse how location in relation to the protected area relates to tree species distribution and diversity.

We found that, compared to soils in the surrounding landscape, soils inside Picos de Europa are characterized by a higher abundance of stones and a thinner humus layer, two important soil parameters associated to plant diversity in forests (Cantero et al., 2003; French et al., 2008; Ren et al., 2012). Stoniness is negatively associated to species richness in the study area, a result in line with previous studies in Mediterranean environments (Ceacero et al., 2012). However, according to our best-ranked models, stoniness is not a relevant variable for tree species diversity. In contrast, topsoil organic matter content shows an important effect, particularly on the Richness index, showing a positive association with species composition. This result, which matches previous studies analysing the effect of organic matter mass in temperate deciduous forests in central Europe (Hårdtle et al., 2003), may explain the lower value of the Richness index of plots inside Picos de Europa. However, topsoil organic matter is not associated in a significant way to the Shannon index, the species diversity indicator that actually differed between protected and unprotected plots.

Our best-ranked models also show an association between species richness and pH soil acidity and plot slope. These results match findings observed in earlier studies analysing the effects of edaphic and topographic factors on species richness (Hårdtle et al., 2003; French et al., 2008; Mod et al., 2016). Still, these two ecological factors are similar in all study plots, for which they do not help to explain differences on species composition between plots in the protected area and outside it.

Finally, we observed lower Shannon index values in plots inside the PA, indicating a more heterogeneous landscape outside Picos de Europa. A possible explanation for this result is the dominance of *Fagus sylvatica* stands inside Picos de Europa, which contrast with the dominance of mixed stands in plots outside Picos de Europa. As beech forests are characterized for conforming monospecific stands (Krämer and Hölscher, 2009), this homogeneity of tree species might result in low values of the diversity Shannon index. Similar differences have been observed in other studies comparing ecological features of near-natural *Fagus sylvatica* stands and communities with less proportion of one dominant tree species (Hui et al., 2011).

Overall, soil's organic matter seems to be the only ecological factor studied contributing to explain the lower species inside the PA. Yet, soil organic matter is not associated to the Shannon index, the only indicator that significantly differed between plots inside and outside the PA. Thus, overall, our results do not show key association between ecological variables and species richness in Liébana forest commons.



## 4.2 Anthropogenic disturbances

The second objective of this study was to quantify differences in human-dominated disturbances between forest commons under the protected status and forest commons outside it, and to analyse how these factors may influence tree species richness distribution in the study area.

Best-ranked models for Shannon and Richness indices show a significant association between tree species composition and anthropogenic disturbances, particularly plot isolation and presence of silvicultural systems. The most important variables in our models are those measuring distance to the nearest path and village, and, with less direct importance, presence of regeneration felling treatments. These findings dovetail with recent research evaluating variables associated to species diversity, which also emphasize the importance of including anthropogenic disturbances in species diversity analyses, particularly in human-dominated landscapes (Guèze et al., 2015; Mod et al., 2016). Five aspects deserve further discussion.

First, the results of the correlation analysis underscore the significant association between species richness and distance to the nearest human settlement, a finding previously reported in tropical forest of Bolivian Amazon (Guèze et al., 2015) and in pine and oak forests across Mexico (Silva-Flores et al., 2016). The finding, however, contrasts with one study in temperate oaks in Spanish Central Pyrenees showing no association between distance to nearest town and *Quercus* spp spatial distribution (Kouba et al., 2011). We argue that these differences in findings probably relate to variations in the socioeconomic characteristics in the study sites, which might have resulted in different impacts on the ecological system (Meyer and Crumley, 2011). Thus, during the second half of the twentieth century, the Pyrenean region suffered an important depopulation and a consequent abandonment of human activities, a phenomena that frequently results in the homogenization of the rural landscape mosaic as woody species colonized abandoned lands (Rotherham, 2013; Viedma et al., 2015; Lavorel et al., 2017). Although the Liébana region also suffered from depopulation during that time –i.e. population decreased by 54% from 1950 to 1981 (Reques, 1997)–, the increasing demand for food supply by the neighbouring industrialized areas favoured the specialization in livestock production of Liébana from the 1970s onwards (González, 2001). Traditional livestock farming operations such as hay making, pruning, or grazing on forest commons allowed the maintenance of a grassland-woodland mosaic, and the biodiversity dependent upon these practices, until the early 2000s. Timber harvest of native deciduous species like *Fagus sylvatica* continued until 1980s, although the twenty century saw a shifting to harvest non-native conifers from the commercial timber-producing plantations established by the State Forestry Administration intervention of public woodlands in Liébana. This shift favoured the co-occurrence of wild and synantrophic species (Ezquerria and Gil, 2004).

Second, our modelling methods show a negative association between distance to nearest town and species diversity, i.e. forest species diversity is higher in areas close to human settlements. This association might be due to the human pressure potentially associated to higher accessibility, as Guirado et al. (2007) also noticed for periurban oak forests of north-eastern Spain, where

presence of recent human disturbances is associated to higher species richness, particularly synanthropic species. Other studies have also linked intensity of human disturbances to the presence of pioneer, non-native species in natural habitats (Battles et al., 2001; Gourlet-Fleury et al., 2013; Bauman et al., 2015). In our study, we observed *Castanea sativa* and *Ilex aquifolium*, species traditionally pruned for the provision of food (chestnuts) and winter fodder, in plots located less than 1000 meters away from towns. We also recorded plantations of the exotic *Pinus radiata* D. Don inside or around accessible plots located less than 650 meters away from human settlements. Inside these plots, we also recorded species untypical for the studied forest habitats, like *Arbutus unedo* L. and *Pyrus* sp. These results may provide further support to the idea that plot isolation does not necessarily result in an enriched forest habitat, as human intervention may sometimes increase the total number of species by introducing atypical species in a community (Helm et al., 2015).

Third, this research also shows a relevant association between species diversity and distance to nearest path, including unpaved roads or walking trails trampling by foot, animals, or wheeled vehicles, but in which vehicle traffic is limited to forest rangers and local inhabitants use. Species diversity bears a negative association distance to nearest path; in other words, forest species diversity is higher in better accessible areas, a finding in line with a recent study analysing the effects of human path, trails, and roads on plant species richness (Root-Bernstein and Svenning, 2018). Nevertheless, distance to path does not significantly differ between plots inside and outside Picos de Europa, for which this anthropogenic disturbance does not assist in explaining differences on species richness between protected and unprotected sites.

Fourth, our findings show that plots inside Picos de Europa tend to present more silvicultural treatments, particularly forest cover improvement treatments, than plots outside the park. Greater forestry operations inside the PA may be counterintuitive for practitioners considering the protection category of National Park as forest reserve where minimal intervention is applied to allow a continued succession and natural disturbances in the forests. In Spain, however, National Parks are actively managed by authorities who implement management strategies oriented to safeguard the natural systems that justified the PA designation (Law No. 30/2014 of Spanish Government). In Picos de Europa, these strategies center around silvicultural activities oriented to preserve the habitats that justified its designation, i.e. Atlantic Forest natural and semi-natural habitats such as *Fagus sylvatica* forest patches (Regional Forest Administration, pers. comm., September 2016). Although Picos de Europa National Park management plan was derogated in 2005 due to a legal action taken by local communities living in the buffer zone (Spanish Government, 2005), silvicultural operations are undertaken under the umbrella of national and regional legislation and European conservation initiatives like the LIFE+ Cantabrian Capercaillie Project (LIFE09 NAT/ES/000513). Thus, weeding and brushing out of trails have been carried out to facilitate the access of visitors to the National Park (Park ranger, pers. comm., September 2016). In addition, the conservation strategy followed by the National Park Administration to promote the presence of the endangered bird subspecies Cantabrian capercaillie (*Tetrao urogallus cantabricus*), considered an umbrella species in montane forest ecosystems (Blanco-

Fontao et al., 2011), includes silvicultural interventions on forest cover practices in an attempt to favour capercaillie's habitat. These silvicultural practices included brush cutting and thinning applied to reduce canopy closure and to facilitate *Vaccinium myrtillus* L. growth, an important food source to capercaillie's populations (Lakka and Kouki, 2009; Mikoláš et al., 2015). Accordingly, we found that plots inside Picos de Europa tend to present more silvicultural treatments, particularly forest cover improvement treatments, than plots outside the park. Overall, silviculture inside the reserve seems to affect tree composition by reducing woody species diversity.

Finally, when studying the influence of silvicultural systems on species' diversity, we find that the only variable with relative importance in our models is the presence of regeneration felling operations, which shows a negative association to the Shannon index. Our results mainly relate to the effects of selective felling, a low-intensity clear-cutting activity practice consistent in an individual-tree selection cutting 'that maintains or develops an uneven-aged forest structure over time' (Lexerød and Eid, 2006, p.503). Several reports have discussed the association of low intensity, close-to-nature silviculture to the presence of vegetation typical of late-successional stages (Battles et al., 2001; Saeki, 2007). On the one side, by benefitting the presence of late-successional ecosystems, selective felling contributes to a higher evenness of the first dominant tree species in the study area, *Fagus sylvatica* (Ministerio de Medio Ambiente, 1997–2007). On the other, when focusing on mixed broadleaf forests, our study brings deeper insights into the assumption that non-intensive silvicultural systems promotes uneven-aged stands that benefit species diversity by increasing vegetation composition associated to late-successional ecosystems of forest sites. Particularly, we observed *Corylus avellana*, as dominant tree species, and *Crataegus monogyna*, as accompanying tree species, in mixed broadleaf forests plots presenting selective felling practices. The latter finding is in line with published studies analysing the effects of selective felling in coniferous and deciduous species, which also consider selective felling as a management practice that favours biological diversity for those forest habitats (Atlegrim and Sjöberg, 2004; Martín-Alcón et al., 2015).

In sum, silviculture inside the reserve seems to affect tree composition by reducing woody species diversity. Among the silvicultural operations considered, presence of regeneration felling practices is the only treatment with relative importance for species' diversity, favouring the evenness of species associated to late-successional ecosystems. Remarkably, the anthropogenic variable distance to town is a key driver of species diversity in the study area, with a higher number of species in plots closer to human settlements.

#### 4.3 Protection status and species diversity interaction in three forest habitats

When comparing species diversity of three different temperate deciduous forest habitats occurring in forests commons inside and outside Picos de Europa, We observe similar tree species pattern for mixed broadleaf forests and Pyrenean oak forests regardless the protection

status. Our findings are in line with Gray et al. (2016) when comparing biodiversity between protected and unprotected areas with the same land use. We argue that the finding is explained by the fact that, despite differences in the protection status, both sites are managed by the Forest Administration of the regional government, who, in the absence of a valid management plan in the PA, applies similar forest management technical criteria inside and outside the protected area (Forest ranger, pers. comm., August 2016).

Interestingly, we found differences in the ecological features of one forest habitat type, *Fagus sylvatica* stands, which have a significant more heterogeneous species composition outside Picos de Europa. Specifically, we observed significant differences for the Shannon, Evenness and Richness indices and for the reciprocal form of the Berger-Parker index (Fig.3), similar to the ones observed by Bilek et al. (2011) when comparing managed and unmanaged beech forests in Central Europe. The low value of Shannon index in the beech forests inside Picos de Europa indicate a single-layered *Fagus sylvatica* composition of these stands, in line with observations in pure beech forests of the Basque Country, a neighbouring region (Peña et al., 2011). Nevertheless, although a high portion of accompanying species may not be considered a natural pattern of beech stands, studies analysing the temporal and spatial dynamics of near-natural deciduous forests dominated by *Fagus sylvatica* show a forest cycle based on 'gap-dynamics', in which species composition oscillate due to small scale disturbances such as canopy openings (Wissel, 1992; Emborg et al., 2000).

Briefly, by promoting the presence of monospecific beech stands without including species associated to the natural small-scale disturbances of these habitats, interventions carried out in beech forests inside Picos de Europa do not seem to contribute to higher stand diversification, plots inside the PA being poorer in terms of species than plots outside the PA.

## 5. Conclusion

Results presented herein show more heterogeneity of forest communities outside than inside Picos de Europa National Park, arguably as silvicultural systems applied inside the designated area benefit the presence of single-layered *Fagus sylvatica* forests. Aiming to provide some management guidelines to favour biodiversity maintenance in this protected area, we recommend the inclusion of practices emulating natural disturbances of beech forests, promoting the appearance of pioneer light-demanding specialist species associated to these forest habitats. This recommendation implies a strategy to enhance the resilience capacity associated to *Fagus sylvatica* ecosystems, particularly relevant in the context of climate change in the study area, which might increase vulnerability to pests and phenological changes of forest habitats (OECC, 2012). Further research under scenarios of climate change is required to attain more integrative management recommendations.

Within the range of management options for promoting tree species assemblages in this forest habitat type, our work brings into consideration the positive influence that human-induced

disturbances hold for increasing tree species richness and evenness. This option might be especially relevant in natural landscapes with long histories of forest use, such as the study site. Our study also reinforces the social-ecological systems approach to biodiversity conservation by providing an example of how the persistence of some stewardship customs and traditional uses of local communities in forest commons of the Liébana valley seem to result in the long-term maintenance of diverse natural habitats and their associated species. We recommend further research to identify which particular forest-related practices performed in forest commons outside Picos de Europa enrich community composition through habitat-specific species.

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#### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at

#### Appendix B. Field plot form

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