Biodiversity patterns in the managed and unmanaged silver fir-beech forests in the western Pyrenees: towards sustainable use

Vlatka Horvat

PhD thesis

Leioa, 2018

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Leioa, 2018

PhD book design and realisation by Antonio Secilla

Acknowledgements

At the end of my PhD I will try to mention and give my sincerest thanks to all the important persons who have been with me throughout these years. Firstly, I owe great thanks to the person who encouraged me to start the PhD, Mercedes Herrera. Muchísimas gracias Meme por transmitirme tu optimismo y por todo lo que has hecho por mí en estos cinco años. Gracias por todas las excursiones, conversaciones, apoyo moral y por cuidarme. This thesis would not have been possible without my two supervisors, Idoia Biurrun and Itziar García Mijangos, great persons and professors with immense patience who supported me during all this time. Muchísimas gracias por todo el tiempo que me habéis dedicado, por compartir vuestro conocimiento, por las identificaciones de plantas, por leer mil versiones del mismo artículo, por todos los consejos, por guiarme en estos cinco años y lo más importante, por vuestro apoyo, comprensión e inmenso cuidado en los momentos duros.

Special thanks to my colleague, Dani, for joining me during field sampling in the Pyrenees and for running up and down the steep slopes for eight days. Gracias Dani por estar conmigo en esos momentos. Gracias a los colegas de laboratorio, Diego, por compartir tu conocimiento y Marta, por corregir mis resúmenes en castellano añadiendo los artículos. Many thanks to the members of the department, who made me feel welcome during these five years: Juan Antonio Campos, Javier Loidi, Isabel Salcedo, and Txema Gorostiaga. Muchísimas gracias por vuestro apoyo, consejos y conversaciones. Gracias Asun por ayudarme con los muestreos! Gracias también a tres preciosos estudiantes: Jorge García de Vicuña, Almudena Pereda y Raúl Ilanduin por acompañarme a muestrear durante diez días con esas sonrisas.

Special thanks to Hanna Tuomisto for all the time dedicated and all the advice given, and to the Amazon team for their warm hospitality during my stay in Turku. Thanks to Patxi Heras and Javier Etayo for their great collaboration in the manuscript writing, for patience in the bryophyte and lichen identification, and for sharing their knowledge. Thanks to Riccardo and Peter for giving up their time to read this thesis. Thank you, Sandro, for your kindness and for correcting my text. Thanks, Francesco and Sabina for all your advice. Gracias Antonio por maquetar la tesis.

Enormes gracias a mis primeros "pisukides", Eider, Pino y Sauer por darme mucha felicidad y por estar conmigo hasta hoy. Thanks to my dear friends for being with me Anka, Gazda, Vujnović, Kika, Vale, Kika, Tomić, Marino, Vid, Nensi, Indi, Josip, Sandra, Robi, Saray, Alex, Esther, Jagoba, Kristina, Mari Paz and Corradino. Thank you, dear president Klaas, for the lovely excursions and for sharing your knowledge. Eskerrik asko Garbiñe y Houria por estar conmigo y cuidarme en los momentos de impotencia.

Thanks to my grandmother Joke for her love and all the Skype conversations. Hvala Vam Joke, Budo i Njanja. The last and greatest thanks I owe to my parents for their love and patience. Bez Vas bilo bi nemoguće i hvala Vam jer ste mi omogućili da radim ono što volim.

Contents

Dissertation summary

Forest exploitation is growing worldwide, and the negative impacts of forest management on biodiversity are well known. To reconcile socio-economic necessities and conservation requirements, sustainable forest management has become one of the important issues in modern forestry, especially in temperate forests, which are one of the most transformed ecosystems in the world. In the last decades, research on sustainable forest management has been based on the study of old-growth forests, which provide adequate knowledge about ecosystem functioning, natural dynamics and biodiversity patterns.

In this context, the present dissertation significantly contributes to our overall knowledge about management impacts on biodiversity. In particular, it is the first study with a focus on the diversity of vascular plants, bryophytes and lichens in western Pyrenean silver fir-beech forests. These forests are particularly interesting because of their management history, which differs from Central European forest management traditions, and because silver fir reaches its southwestern distribution limit in the western Pyrenees.

The introduction part of this dissertation explains all important ecological points in silver fir-beech forest functioning, such as natural forest dynamics and ecological requirements of vascular plants, bryophytes and lichens. It also includes a summary of the forest management issues, with details about management history and typology.

The second chapter reveals the patterns of vascular plant species diversity across different management types. Four management categories were established, according to the time after the abandonment of forest management. The vascular plants were classified into different groups regarding their habitat preference (forest specialist, forest-edge species, generalists and open area species) to test whether different groups respond differently to management types. The results of this study confirmed that management, although weakly, affects vascular plant diversity, both regarding species richness and species composition. Apart from forest management, continentality and forest gaps were also important drivers of species richness and composition.

The knowledge about the impact of forest management gained in the second chapter was used in the third chapter, which focused on bryophyte diversity. In this chapter, I only considered three management types, based on management intensity. According to the results, intensively managed forests have lower

species richness and are generally located at lower elevations, which is the main driver of bryophyte richness and turnover. Lastly, Dierssen's bryophyte classification regarding forest management was tested, and the results showed that this classification is not suitable for western Pyrenean forests.

As chapters 2 and 3 appointed forest management as an important driver for plant diversity, the necessity of a detailed forest structure analysis to draw sounder conclusions emerged. Thus, chapter 4 is dedicated to the detailed description of forest structural features and the evaluation of studied forests in the light of sustainable forest management. For this purpose, I used a new sampling design aiming to describe in detail the differences between managed and unmanaged forests. The most representative stands of managed and unmanaged forests were selected; hence, the variable management was reduced to two levels. The results indicate that the managed stands have not been intensively managed in the past and that the variety of management types used has preserved the recommended diameter distribution. Our results also showd that the unmanaged stands are still on the way to develop old-growth attributes because management abandonment is too recent for significant changes in forest structure.

Chapters 2, 3 and 4 served as a basis for chapter 5, which compares vascular plant and bryophyte species diversity, using the same sampling design as in the forest structure assessment, limited to two levels of forest management. For this chapter, additional variables, related to soil properties and forest structure, were introduced. The need for the inclusion of these new variables emerged from the results obtained in the second and third chapters on plant diversity, in which the geographical distance played a role in species turnover, as the percentage of variance explained by space might also be attributed to unmeasured environmental variables. My results suggest that vascular plants and bryophytes respond differently to environmental variables, although elevation was one of the most important drivers both for vascular plant and bryophyte richness. Forest structure did not play any role in plant diversity, except for the number of large fir trees, which was one of the drivers for vascular plant species turnover.

To complement our knowledge about the impacts of forest management on plant diversity, lichens were also tested as potential indicators. The last chapter describes the study conducted to assess the response of lichen diversity to forest management and the lichens' indicator values for unmanaged forests. The sampling design was once again based on two management categories, and topographic, climatic and forest structural variables were taken into account. Based on the results, lichen species richness can be related to slope, but forest management also plays a role in lichen species turnover. I suggest that rare lichen species from the *Lobarion* community can be used as indicator species of unmanaged Pyrenean forests.

Resumen

La explotación forestal está incrementándose en todo el mundo, siendo bien conocido su impacto negativo en la biodiversidad. El concepto de "gestión forestal sostenible" ha irrumpido con fuerza en la silvicultura moderna con el objetivo de reconciliar las necesidades socio-económicas y de conservación. En las últimas décadas la investigación ligada a la gestión sostenible se ha basado en el estudio de los denominados "bosques antiguos", que proporcionan conocimientos indispensables sobre el funcionamiento de los ecosistemas, la dinámica natural y los patrones de la biodiversidad. Dichos estudios son considerados de gran utilidad para el desarrollo de estrategias sostenibles de gestión forestal, especialmente en los bosques templados, uno de los ecosistemas más transformados del mundo.

En este contexto, la presente tesis supone una contribución al conocimiento general sobre el impacto de la gestión forestal en la biodiversidad. En concreto, se estudia por primera vez la diversidad de plantas vasculares, briófitos y líquenes de los hayedo-abetales del Pirineo occidental. Estos bosques son especialmente interesantes debido a su particular gestión histórica, que difiere de la gestión forestal tradicional llevada a cabo en los países centroeuropeos. Su interés radica también en el hecho de que el abeto alcanza su límite de distribución suroccidental en el área de estudio.

La tesis comienza con un primer capítulo introductorio que presenta los aspectos ecológicos más importantes en el funcionamiento del hayedo-abetal, tales como la dinámica forestal natural y los requerimientos ecológicos de las plantas vasculares, los briófitos y los líquenes, así como un breve compendio de la gestión forestal, incluyendo su historia y su tipología.

El segundo capítulo pone al descubierto los patrones de la diversidad de plantas vasculares en relación con el tipo de manejo empleado. Se establecieron cuatro categorías de manejo en función del tiempo transcurrido desde la última actividad forestal y del tipo de manejo. Las plantas vasculares fueron clasificadas según sus preferencias ecológicas en cuatro grupos: especialistas forestales, especies de orla, generalistas y de espacies abiertos, para así poder testar si los diferentes grupos de plantas responden de forma diferente a la explotación forestal. Los resultados de este estudio confirmaron que la explotación forestal afecta, si bien débilmente, a la diversidad total de plantas vasculares, tanto en lo que respecta a la riqueza de especies como a su composición. Además del

manejo forestal, la continentalidad y la presencia, abundancia y tamaño de los claros forestales también resultaron ser factores importantes para la riqueza y composición de especies.

El tercero capítulo se centra en la diversidad de los briófitos. Para este estudio se redujeron las categorías de manejo a tres, en base a la intensidad de la explotación forestal. Según nuestros resultados, la altitud es el factor principal que afecta tanto a la riqueza como al cambio en la composición florística. Asimismo, los bosques intensivamente manejados presentan una menor riqueza de briófitos. Por último, se concluye que la clasificación de briófitos según su respuesta a la explotación forestal realizada por Dierssen no es adecuada para los bosques del Pirineo occidental.

Los resultados de los capítulos 2 y 3 mostraron que el manejo forestal es un factor que afecta a la diversidad florística, lo que nos sugirió la necesidad de analizar la estructura forestal para obtener una visión más completa. El cuarto capítulo se centra en la descripción detallada de las características estructurales de estos bosques, así como en su evaluación desde la perspectiva de la gestión forestal sostenible. Con el objetivo de establecer las diferencias estructurales de los bosques no manejados frente a los manejados se seleccionaron los bosques más representativos de ambas categorías. Nuestros resultados indican que estos bosques no han sufrido en el pasado un manejo muy intensivo, y que los tipos de manejo aplicados han conservado la distribución de diámetros recomendable. Nuestros resultados también sugieren que los bosques no manejados están todavía en el proceso de desarrollar las características estructurales de los bosques antiguos debido a que el abandono del manejo es todavía demasiado reciente.

Los capítulos anteriores formaron una base sólida para el capítulo 5, que consiste en un estudio comparativo de la respuesta de la diversidad de plantas vasculares y briófitos en relación al manejo forestal. Se utilizó el mismo diseño de muestreo que en el capítulo 4, con dos niveles de manejo. Además de las variables estructurales se incluyeron variables edáficas. La necesidad de incluir estas nuevas variables surgió de los resultados obtenidos en el capítulo 2 y 3 sobre el papel de la distancia geográfica en el recambio de plantas vasculares y briófitos, debido a que parte de varianza explicada por el espacio podría también ser atribuida a variables ambientales no medidas. Los resultados obtenidos en el capítulo quinto sugieren que las plantas vasculares y los briófitos responden de forma diferente ante las variables ambientales, si bien la altitud resultó uno de los factores más importantes para la riqueza de ambos grupos de plantas. La estructura no juega ningún papel en la diversidad de plantas, si exceptúamos al número de abetos grandes, que ha resultado ser uno de los factores que afectan al cambio en la composición de plantas vasculares.

El capítulo 6 describe el estudio realizado para evaluar la respuesta de la diversidad de líquenes a la explotación forestal, asi como su valor indicador respecto a los bosques no manejados. El diseño del muestreo se basa en las dos categorías de manejo forestal, e incluye el uso de variables topográficas, climaticas y estructurales. La riqueza de especies de líquenes está relacionada con la pendiente, mientras que la explotación forestal juega un papel determinante en el recambio de especies. Se sugiere que las especies raras de la alianza *Lobarion* pueden ser consideradas indicadoras de los bosques pirenaicos no manejados.

chapter 1

Vlatka Horvat (2018) PhD THESIS pp. 19-30

1. General introduction and objectives

This dissertation is the result of a detailed research about the impacts of forest management on forest structural features and the diversity of vascular plants, bryophytes and lichens in silver fir-beech forests in the western Pyrenees. As research on the relationship between biodiversity and forest management is one of the crucial topics in forest ecology, the present work should be seen as a contribution to the general understanding of European silver fir-beech forest functioning. This issue has already been faced in several European regions (Paillet et al., 2010), but has never been set out in the western Pyrenean forests. Although detailed floristic and phytosociological studies have been carried out in these forests (Villar, 1980; Etayo, 1989; Rivas-Martínez et al., 1991; Delgado and Ederra, 2013), the management effect on biodiversity has largely been neglected. The importance of this thesis lays on the detailed analyses of biodiversity patterns of western Pyrenean silver fir-beech forests, which mark the distribution limit of these forests in southwestern Europe. Forest management effects were assessed on two different aspects of diversity, species richness and species composition, taking into account relevant environmental factors. Additionally, the stand structure patterns in managed and unmanaged forests were analysed.

1.1. Forest management and its influence on species diversity

Human interventions in the landscape have changed entire ecosystems, especially European forests, which have been exploited since prehistoric times (Ritter, 2011). Over time, and especially in the last century, forest exploitation was intensified and expanded, and forest cover drastically decreased. As a consequence of the century-long intensive forest management, completely untouched or true virgin forests as such have disappeared in Europe (Burrascano et al., 2013), if we accept the terminology according to which a true virgin forest should not have been influenced by people even in the distant past (Peterken, 1996; Gilg, 2004; Burrascano, 2010). According to Silander (2001), only 1% of the northern hemisphere's temperate broad-leaved forests is considered in primary conditions. However, there are still well-preserved forest remnants or old-growth forests which can reflect primary forest conditions. In Europe, most representative old-growth forests may be found in the Carpathian and Balkan regions (Leibundgut, 1982; Korpel, 1995). In any case, there is an existing confusion in the literature regarding the nomenclature for these types of forest remnants. I agree with Burrascano (2010) on the use of the term "old-growth forest" to refer to a subset of natural forests developing only under a limited set of circumstances, mostly associated with long periods without major natural or anthropogenic disturbances (Bauhus et al., 2009; Wirth et al., 2009). As they are subject to natural dynamics, these old-growth forests are characterised both by high levels of structural heterogeneity (Nilsson et al., 2003; Nordén and Appelqvist, 2001) and biological diversity (Franklin and Spies, 1991), which are largely absent in managed forests (Burrrascano et al., 2013; Paillet et al., 2015). For this reason, old-growth forests are an important reference point when evaluating human impacts on forest ecosystems (Peterken, 1996).

Understanding the natural dynamics of old-growth forests has been considered the basis for developing natural disturbance-based (North and Keeton, 2008) or close-to-nature (Commarmot et al., 2005; Heiri et al., 2009) silvicultural systems, able to emulate natural processes and fulfil socio-economic goals while maintaining a full range of late-successional ecosystem services (Franklin et al., 2002; Bauhus et al., 2009). All these terms of silvicultural methods are linked to the concept of sustainable forest management, which was officially defined and approved in the second Ministerial Conference on the Protection of Forests in Europe (MCPFE) in Helsinki in 1993 (resolutions H1 and H2; MCPFE, 1993). However, prior to the definition of sustainable management, forests have often been intensively managed, and the consequences of such an approach may be still evident for decades. The impacts of such historical and also present forest management strategies on forest biodiversity are still poorly understood. A better understanding of biodiversity drivers is, however, mandatory to ensure conservation and appropriate management of forest ecosystems. Besides, the sustainability of forest management should be evaluated taking into account all the relevant aspects, including biodiversity.

The most important feature to evaluate forest management sustainability is forest structure, which determines overall microclimatic conditions below the forest canopy (von Arx et al., 2012). Strongly depending on management type and intensity, forest structure has been considered a key factor determining overall biodiversity patterns (Gao et al., 2014). Thus, assuming differences in forest structural features between managed and unmanaged stands, different patterns of species diversity can be expected, in particular for vascular plants, bryophytes and lichens. In temperate forests, the understory contains the major part of plant diversity, as this layer comprises vascular plants and bryophytes (Lesica et al., 1991; Gilliam, 2007). The forest herb layer is usually less studied than the dominant tree layer (Gilliam, 2007), and the diversity of bryophyte or lichen layer is even less investigated (Glime, 2013; Bagella, 2014). Vascular plants, bryophytes and lichens are equally important members of forest ecosystems, but they may respond differently to environmental factors (Ingerpuu et al., 2003; Bacaro et al., 2008) as they differ in several fundamental traits, including the pathways of nutrient and water uptake (Cornelissen et al., 2007). Consequently, vascular plants, bryophytes and lichens may respond differently to forest management, providing complementary data for the assessment of management effects (Økland et al., 2004; Lalanne et al., 2010).

Vascular plants form the herb layer and the canopy and play a special role in maintaining the structure and function of forests (Gilliam, 2007). The main ecological functions of the herb layer are to provide habitat and forage for many wildlife species and it also has a strong influence on forest nutrient fluxes, successional patterns and the understorey light regime (Augusto et al., 2003; Royo and Carson, 2006; Messier et al., 2009). The herb layer interacts with the overstory, as it can affect tree seedlings and future tree composition, although tree composition can also influence herb layer diversity as well as soil fertility (Muller, 2003: Neufeld and Young, 2003). Different management systems (e.g. even-aged and uneven-aged management) have been investigated in the context of this interaction between the herb layer and the tree composition of the overstory (Paillet et al., 2010; Duguid and Ashton, 2013). Forest exploitation may change forest structure and overstory composition, influencing light conditions, nutrient cycling and ground microclimate, consequently changing species diversity patterns (Bobiec, 1998; Decocq et al., 2004).

Bryophytes are often neglected in vegetation surveys (Bagella, 2014), although they are an integral component of forest ecosystems (Lesica et al., 1991). They increase the structural complexity, play a role in nutrient cycles and moisture retention and provide habitat for other taxa (Rhoades, 1995; Cornelissen et al., 2007; Jonsson et al., 2015). Nevertheless, the overall knowledge about the role of bryophytes in most ecosystems is still limited (Glime, 2013). Even less is known about the fact whether bryophytes are, and to which extent, indicators of forest management. Hitherto, it has been reported that bryophyte assemblages in forest ecosystems are driven by climatic factors (Sun et al., 2013), but also by forest continuity (Frego, 2007), historical factors (Fritz and Brunet, 2010) and tree logging (Nelson and Halpern, 2005; Kantvilas et al., 2015). Bryophytes are considered good ecological indicators due to their sensitivity to environmental changes because of their specific characteristics such as the lack of true roots and waxy cuticles (Gignac, 2001; Pharo and Zartman, 2007). In the same way as vascular plants, forest management may affect bryophytes species diversity as they are sensitive to changes in forest structural features, microclimate, dead wood availability and forest continuity (Peterken, 1996; Bengtsson et al., 2000; Paillet et al., 2010). In fact, the prevailing view is that bryophytes are more sensitive to forest management than vascular plants (Barkman, 1958; Carlberg et al., 1983).

Lichen species play another important part of forest biodiversity in European temperate forests (Coppins and Coppins, 2005) and are considered valuable bioindicators (Rose, 1992; Nascimbene et al., 2007; Aragón et al., 2010) for the evaluation of forest management impacts because of their sensitivity to air pollution (Nimis et al., 2002), forest habitat quality (Kuusinen and Siitonen, 1998; Pykälä, 2004; Bergamini et al., 2005), air humidity (Sillett et al., 2000) and changes in light conditions (Gauslaa and Solhaug, 1996; Ódor et al., 2013). Lichen diversity patterns are also regulated by tree size (Fritz et al., 2008; Lie et al., 2009), which is determined by the forest management system (Nascimbene et al., 2007).

1.2. Management in the silver-fir beech forests

In the European mountains, beech forests have been used since the Neolithic, and human practices have changed the landscape via fires, wood extraction, agriculture and animal husbandry (Peters, 2013). Such forest use was changed around 1700, when forest management started to be an organised rational commercial activity in Central Europe (Hahn and Fanta, 2001). The idea of an organised forest management from 1700 onwards has also included a first preliminary concept of sustainability. Nevertheless, with population growth and other historical events, the idea of sustainable forestry has not been respected. Indeed, many European forests have been overexploited via the clearcut method, which was a usual and economically effective way of timber harvesting from 1800 until recent times (Hahn and Fanta 2001). As a consequence of the different political, economic and forestry development since the 1700s and especially in the second half of the 1900s, divergent forest management histories have been recognised in European countries (Peters, 2013). After 1980, the modern age of forestry started in most of the European countries, integrating ecological, conservation, social, economic and environmental aspects within a multifunctional management system. Although modern forestry methods have come into practice approximately 40 years ago, the tracks of past forest practices are still evident in European countries.

Despite the large body of literature describing the theory of management systems and their variations, two main types can be distinguished, namely even-aged and uneven-aged management (Bončina, 2011; Kuuluvainen et al., 2012). Even-aged forest management creates stands with even tree age structures, as a consequence of clear cutting for forest regeneration (Figs. 1, 2). This type of logging is practiced across different spatial grains, and retention trees might be left on the clear cuts for the following rotation period. This management approach is a repetitive cycle of distinct phases, namely regeneration, growing, thinning and final harvesting, and several silvicultural practices are used to maintain an even-aged structure. In contrast, uneven-aged forest management is a fine-grain forest management strategy maintaining an uneven tree age structure by selective tree logging. There are two types of tree selection,

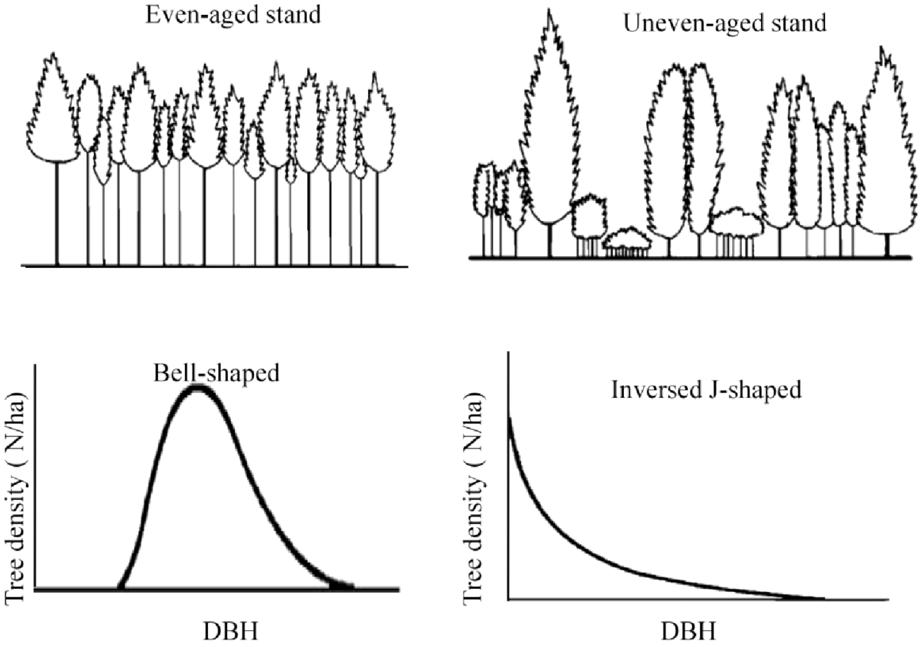

Fig. 1. Scheme of the even-aged and uneven-aged stand managemet systems and their corresponding diameter distributions (from Ganz, 2000).

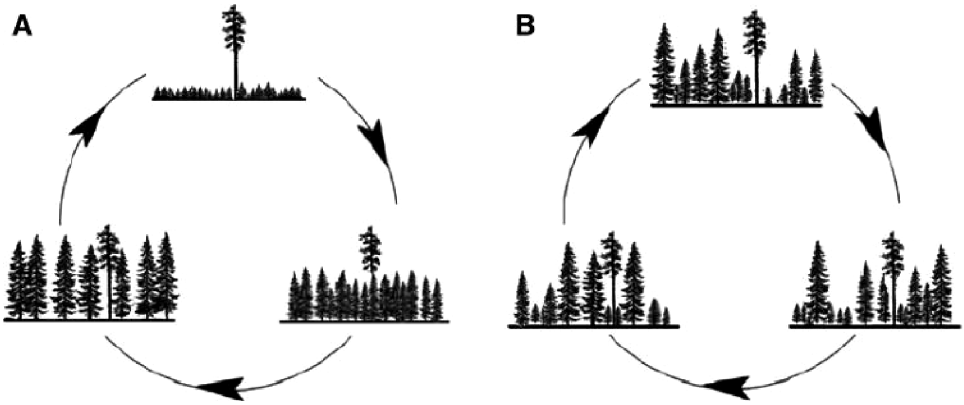

Fig. 2. An illustration of even-aged (**A**) and uneven-aged (**B**) forest management and their phases (from Kuuluvainen et al., 2012).

namely individual logging (single-tree selection) or group logging (group selection) (Nyland, 2002). If the management system applied is single-tree selection, the DBH distribution often corresponds to an inverse J-shape, which is recommended to guarantee ecosystem stability (Fig. 1). In the case of group selection, spatially segregated groups of tree age classes are created. Such a management system, based on tree selection, is generally recommended for biodiversity conservation purposes in beech forests (Schall et al., 2017), as it retains a continuous forest cover and emulates small-scale disturbances (Fig. 2). The above-mentioned management systems should be seen as the basic silvicultural systems, although many versions of these systems have been developed for forest management, depending, among other factors, on tree species composition, regeneration success and topography.

1.3. Study area

The Pyrenean mountain range separates the Iberian Peninsula from the rest of the European mainland, forming a natural border between Spain and France. This mountain range extents in the west-eastern direction from the Bay of Biscay in the Atlantic Ocean to the Mediterranean Sea. Biogeographically, the Pyrenean mountains belong to the Alpine region and, according to the Global Bioclimatic Classification System developed by Rivas-Martínez (2007), the bioclimate is temperate oceanic, with a mean annual temperature of 8°C, mean annual rainfall of 1419 mm and a W-E continentality gradient. The western Pyrenees show oceanic features, with high precipitation along the year, whilst continentality is highest in the eastern Pyrenees.

The present study was conducted in the western part of the Pyrenean mountains, specifically in the Spanish part of the massive, encompassing the provinces of Navarre and Aragón (Fig. 3). The landscape is characterised by mountains and valleys with the dominant bedrock formed by limestone and marly flysch, which correspond to the secondary and tertiary cover over the

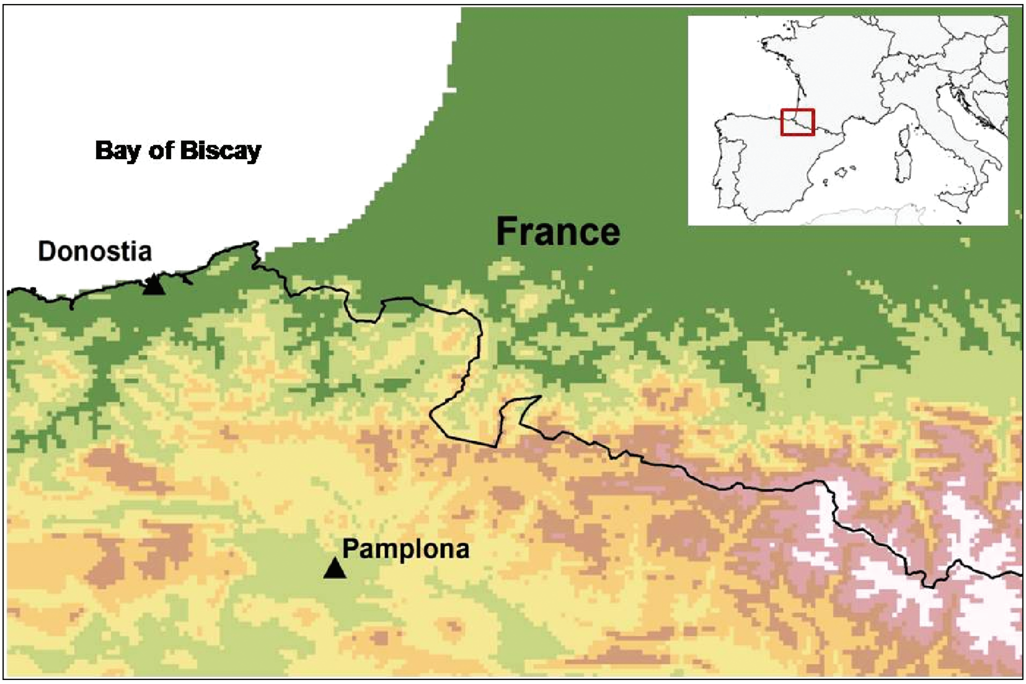

Fig. 3. Location of the study area in the western Pyrenees.

Palaeozoic central axis of the Pyrenees (Loidi et al., 2011). The long history of livestock raising and forest exploitation has considerably shaped the landscape of this area. Consequently, there is a large landscape heterogeneity, with semi-natural grasslands, scrublands, natural forests and *Pinus sylvestris* plantations.

Several types of natural forests are arranged along the elevational gradient. On the valley bottoms, the potential mixed forests with ash (*Fraxinus excelsior*) and several other trees have mostly been replaced by crops and meadows. Only narrow fringes remain near streams and rocky slopes. On the slopes, forests dominated by downy oak (*Quercus pubescens*) prevail, specially on the southern slopes. At higher elevations, but still in the montane belt, beech forests replace oak forests, first on the northern slopes and finally everywhere. Over approximately 1700 m, subalpine forests with *Pinus uncinata* are the only forest type, and beyond the treeline, at elevations over 2200 m, alpine pastures and dwarf shrub communities dominate the landscape (Loidi and Báscones, 2006).

The beech belt is a unique feature, because the silver fir reaches its southwestern distribution limit in these western Pyrenean mountains, where it grows in mixed stands together with beech and even dominates some stands. The silver fir-beech forests of the area are included in the association *Scillo lilio- hyacinthi-Fagetum sylvaticae* Br.-Bl. ex O. Bolòs 1957, which encompasses omprophilous hyperhumid forests growing on calcareous bedrock (Rivas-Martínez et al., 1991). These basophilous beech forests are included in the alliance *Fagion sylvaticae* Luquet 1926, with *Galium odoratum*, *Carex sylvatica* and *Dryopteris filix-mas*, among others, as diagnostic species (Willner et al., 2017). The presence of species such as *Helleborus viridis* subsp. *occidentalis*, *Saxifraga hirsuta*, *Scrophularia alpestris*, and *Scilla lilio-hyacinthus* allows these forests to be included into a geographic variant which corresponds to the suballiance *Scillo lilio-hyacinthii-Fagenion sylvaticae* Oberdorfer ex Rivas-Martínez 1973 (Willner et al., 2017).

These silver fir-beech forests are recognised as an important habitat (Peralta et al., 2013) and included in the network Natura 2000 in the Navarre region and in the natural parks in the Aragón region. Two forests from the western Pyrenees, Lizardoia and Aztaparreta, deserve the highest status of protection and have been declared strict reserves, belonging to the UNESCO World Heritage Site “Primeval Beech Forests of the Carpathians and other Regions of Europe” (whc.unesco.org).

1.3.1. Forest management in the study area

Management of the western Pyrenean silver fir-beech forests has probably started relatively early, comparable to that of European beech forests. Traditional activities in the Pyrenean forests included cattle grazing and extraction of wood for the needs of the local population (Pèlachs and Soriano, 2003). The recent history of forest management started in 1829 with the approval of the first management plan for the forest *Selva de Irati* (Distrito forestal de Navarra, 2007), which only included the western part of the studied area. This first organised forest management strategy in the Pyrenees, proposed by marine officers, was focused on wood extraction for ship construction and consisted of timber exploitation by thinning. With this target management, intensive logging was conducted around 1850. In 1905, the first forest inventory was developed, which planned even more intensive logging until 1930. After these events, the management type and logging intensity have remained unclear. Because of such irregular forest practices, there are no clear conclusions about the management history in this period. The present management plan was approved in 1961 and revised in 1974 and 1996, but without any evaluation about silvicultural practices in the past. A comparison of the first forest inventory from 1905 with the current one reveals that the western limit of silver fir and the cover of other broadleaved species have not changed whereas differences in the quantity of silver fir trees are observed, as silver fir underwent heavy logging in the 19th century. Besides this intensive industrial forest management for wood exploitation, these stands were also used for animal husbandry and charcoal production. These forests can therefore be considered as overexploited and overgrazed in the 19th and early 20th centuries. However, these activities were abandoned between 1938 and 1950, and the forests have started to recover, which is reflected in an increased biomass.

All the above-mentioned activities have not been carried out homogeneously across the territory, because the management type mainly depended on stand accessibility and the possibility of wood extraction. The most intensive loggings in the western part of the studied area were performed in the areas near the rivers, which facilitated wood transportation. Such logging and wood transportation along rivers was applied between 1908 and 1938 and consisted in heavy logging of all silver fir and beech trees with a DBH over 40 cm. In areas far from the rivers, another type of thinning was applied, oriented towards the logging of all trees below 40 cm DBH every 25 years. The consequences of this target management are modifications of the tree layer composition and of the forest structure. In 1940-1950, a new technique for wood extraction by cable red was implemented, which permitted logging in unmanaged areas. All trees larger than 35 cm DBH were logged. Another type of management applied was coppicing, a logging type which allows the stumps to regenerate for up to 25 years; the resulting stems are then harvested. However, coppicing was not overly important in these stands and was only applied in one relatively small area of 56 ha used for charcoal production.

In this context, it can be concluded that until 1950, the forests in the western part of the studied area were managed as even-aged by clearcutting and intensive thinning. As these aggressive methods proved to be unsustainable for the ecosystem and did not yield the expected results, they were abandoned after 1950. Since then, the forest management system has significantly changed: low intensity logging as salvage logging of sick trees and logging of the largest trees have been applied to improve stands.

Not all western Pyrenean forests were included in the management plans of the last century. In fact, many patches of forests situated at the highest elevations were inaccessible until 1970, when the first roads were built. Therefore, before 1970, the management of these forests was oriented towards animal husbandry and wood extraction for personal use and latter abandoned. These forests are nowadays included in natural parks and represent the best-preserved forests in this area.

1.4. General objectives and dissertation structure

The integrated assessment of the impacts of forest management on the diversity of vascular plants, bryophytes and lichens is still scarcely investigated (Johansson, 2008) and, to my knowledge, unknown for Pyrenean forests. Thus, this study may provide valuable insights into the sustainable management of European forests and offers a basis for effective conservation policies in the study region.

The thesis explores several aspects of plant and lichen diversity regarding forest management and environmental factors in the silver fir-beech forests from the western Pyrenees; the specific objectives are as follows:

1. To determine the drivers of vascular plant, bryophyte and lichen species richness and turnover in the silver fir-beech forests from the western Pyrenees;

2. To determine the richness and turnover drivers of different functional groups of vascular plants, bryophytes and lichens in the silver fir-beech forests from the western Pyrenees;
3. To assess the management effects on the vascular plant, bryophyte and lichen diversity in the silver fir-beech forests from the western Pyrenees;
4. To explore the indicator species of managed and unmanaged stands in the studied area;
5. To describe and analyse the differences in forest structural features between Pyrenan managed and unmanaged stands

Thesis structure

Chapter 1 provides an overview of forest management issues, describes the study area in detail and outlines the specific aims of the study. Chapter 2 presents the results regarding the effects of forest management on vascular plant diversity, taking into account climatic and topographic factors. I also explored vascular plant responses to forest management in terms of habitat preference; the results of this study were published in the journal *Forest Ecology and Management* in February 2017. Chapter 3 analyses the effects of forest management strategies on bryophyte diversity and their specific groups regarding taxonomy, life-form and sensitivity to forest management. This work was published in the journal *Biological Conservation* in November 2017. Chapter 4 is dedicated to the description, analysis and comparison of forest structural features of managed and unmanaged Pyrenean forests. This article is under review in *iForest,* submitted in January 2018. In Chapter 5, vascular plant and bryophyte species diversity are compared regarding forest structural features as well as edaphic, topographic and climatic variables. This study is currently under preparation and ready for submission. The effect of forest management on lichen species diversity is assessed in Chapter 6. In this work, the indicator value of lichen species is explored, with a focus on rare species. This last study is currently under review in the journal *Ecological Indicators*, submitted in January 2018.

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Vlatka Horvat (2018) PhD THESIS pp. 31-58

Herb layer in silver fir – beech forests in the western Pyrenees: does management affect species diversity?

ABSTRACT

Silver fir-beech forests form ecologically important ecosystems in European mountains, where they have been intensively managed due to timber harvesting. Forest management effects can be evaluated using herb layer diversity as an indicator of environmental changes. Therefore, revealing the patterns of herb layer diversity is necessary for developing strategies for sustainable management. Knowledge on management history of fir-beech forests in the western Pyrenees is still limited. In this study we aim to disentangle the environmental drivers of species richness and species composition of these forests emphasizing the role of forest management. We sampled the herb layer vascular plants in 68 plots distributed among 14 silver fir-beech stands of the association *Scillo lilio-hyacinthi-Fagetum sylvaticae* and related diversity patterns with management histories, light conditions and topographic and climatic variables. Four management categories were established: *recently managed*, *long managed*, *recently abandoned* and *long abandoned*. Species richness was analysed by GLMM and species composition by partial CCA and PCNM. Multivariate dispersion analysis was used to assess differences in beta diversity among management categories. Management, continentality and slope had in general a weak effect on species richness, continentality with a positive effect whilst slope and management, in category of *recently abandoned* stands, with a negative effect. In addition, the percentage of large gapshad a moderate effect on *open area* species richness. Species composition was related to slope, ombrothermic index, forest management and spatial effects in terms of neutral processes. *Long managed* forests showed differences in beta diversity with *recently abandoned* and *long abandoned* forests. Our study suggests that environmental variables in combination with spatial effects are the main drivers of species diversity at small sampling scale, highlighting that management plays an important role in these western Pyrenean silver fir-beech forests.

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KEY WORDS **Abandoned forests; Beta diversity; Hemispherical photography; Managed forests; Southwest Europe; Species richness**

PUBLISHED ***Forest Ecology and Management* 385, 87-96 (2017)**

ABBREVIATIONS AIC, Akaike Information Criterion; CCA, Canonical Correspondence Analysis; FE, Forest edge species; FS, Forest specialists; GLMM, Generalized Linear Mixed Model; GS, Generalists; LAI, Leaf Area Index; LA, long abandoned; LM, long managed; OA, Open area species; PCNM, Principal coordinates of neighbour matrices; RA, recently abandoned; RM, recently managed; VIF, Variance inflation factor.

1. INTRODUCTION

Silver fir-beech forests form ecologically important ecosystems in European mountains (Peterken, 1996) from the East Carpathians to the Pyrenees and from the Beskids in Poland to the mountains of northern Greece (Konnert and Bergmann, 1995). Being of high importance for timber harvesting, these forest ecosystems are transformed more than any other forest biome (Hannah et al., 1995). This fact has given rise to studies about the effects of management on species diversity in these forests, in particular on the diversity of the herb layer, which is widely recognised as an important component of the forest ecosystem and its functioning (Gilliam, 2007) and contributes the most to forest plant diversity in temperate forests (Roberts, 2004). As such, it can be used as a measure of environmental changes and human disturbances (Schmidt and Weckesser, 2002). Therefore, understanding the mechanisms that drive herb layer plant distribution is essential for the development of management strategies in temperate forests (Sabatini et al., 2014). In this context, numerous studies in the last decades have been dedicated to herb layer investigation, with the objective to emphasise its role in forest functioning (Brumme and Khanna, 2009).

Forests are complex ecological systems (Kuuluvainen, 2009) and many factors drive herb layer diversity: combination of abiotic constraints, biotic interactions and disturbances in space and time. Overall mechanisms that drive plant distribution can be summarised in the frame of two theories, niche-based processes (Tilman, 1982) and neutral processes (Nabout et al., 2009). With regards to niche-based processes, previous studies broadly define the main factors that affect herb layer diversity in forests, such as light transmittance and soil water supply (Augusto et al., 2003; Härdtle et al., 2003; Barbier et al., 2008) or forest management (Ramovs and Roberts, 2003). Neutral processes (Hubbell, 2001) include variation in species related to random dispersal and ecological drift (Legendre and Legendre, 2012). Regarding this issue, recent studies have considered both niche and neutral processes as determinants of species diversity (Chase, 2005; Legendre et al., 2009), stressing that relative contribution of these may vary with the spatial scale of analysis (Chase and Knight, 2013).

Among niche-based processes, several studies have highlighted the important role of forest management in Central European beech forests by comparing plant species diversity in managed and unmanaged forests (Brunet et al., 2010). The meta-analysis provided by Paillet et al. (2010) showed that the species richness of vascular plants tends to be higher in managed forests, although the response was heterogeneous, probably due to the contrasting results obtained at the local scale (Schmidt, 2005; Sebastià et al., 2005; Burrascano et al., 2009). These inconsistencies when comparing managed and unmanaged stands across different regions might be the consequence of the lack of detailed information about silvicultural practices (Roberts and Gilliam, 1995). In other words, forest management histories differ among European countries because beech forests have been harvested for centuries by different methods and with different intensities (Peters, 2013).

The present study addresses the issue of forest management effects on the herb layer species diversity for silver fir-beech forests from the western Pyrenees, where silver fir reaches its south-western distribution limit. Although silver fir-beech forests in the western Pyrenees have been studied at large in a floristic sense (Villar, 1980a; Rivas-Martínez et al., 1991), no studies about herb layer diversity and its relation with forest management have been performed to date. The case of the western Pyrenean forests is a complex issue regarding forest management because of unsystematic silvicultural practices conducted in the last two centuries and lack of data. While in south-eastern Europe and in Alpine Regions, silver fir-beech forests have been managed by selective logging in the last two centuries (Hahn and Fanta, 2001), in the western

Pyrenees, little is known about management history of these forests. Undoubtedly, it was strongly linked to animal husbandry, which significantly influenced forest cover and landscape connectivity. Forest exploitation basically consisted in rather arbitrary logging, depending on local population needs and wood demand. In the last 50 years, animal husbandry and forest management have become less intense because of human migrations and the abandonment of these activities, which led to an increase in forest biomass and landscape changes (Vicente-Serrano et al., 2000). Following the law approval on forest management regulation for this area in the 1970s, forest management became systematic and organised, although some areas remained out of forest inventory and management plans. At the same time, remote and better preserved forests were declared protected areas, such as natural parks and the strict reserve Aztaparreta*,* whichwas firstly described as virgin forest (Villar, 1980b), but nowadays it is considered an old-growth forest with well developed old-growth attributes without any evidence of past management practices. Because of the valuable information that old-growth forests can provide about natural disturbance processes (Peterken, 1996), this old-growth forest can be taken as a reference when studying plant diversity and tackling forest management issues.

Although the effect of forest management on herb-layer diversity has been addressed in several studies, more research at the local scale is needed in order to obtain sound conclusions through meta-analyses (Paillet et al. 2010). In this context, the present study could contribute to a better general understanding of this issue, moreover if we consider the relevance of these western Pyrenean forests as south-western distribution limit of European silver fir-beech forests. The unsystematic forest management of Pyrenean forests has supposed an additional challenge in our study, which we have tried to clarify in order to better assess its influence on plant diversity.

According to the current literature about forest management effects in silver fir-beech stands in Europe, we expected that forest management would affect species richness and species composition. In particular, due to overall management abandonment of Pyrenean forests, we expected species richness to decrease, although this general pattern may be sensitive to landscape patterns and management history (Paillet et al., 2010). Given the above, the purpose of the present study is to reveal the role of forest management on herb layer diversity in western Pyrenean silver fir-beech forests. We analysed species diversity regarding both species richness and species composition. This study aims to answer (1) which environmental factors drive species richness in silver fir-beech forests from the western Pyrenees? (2) Which factors explain the variation in species composition in these forests? (3) Does management affect species diversity?

2. MATERIAL AND METHODS

2.1. Study area

The study area is located in the Spanish part of the western Pyrenees (Fig. 1), in the regions of Navarre and Aragón. The landscape is characterised by mountains and valleys with dominant bedrock formed by limestones and marly flysch, which correspond to the Secondary and Tertiary cover over the Palaeozoic central axis of the Pyrenees (Loidi et al., 2011). Biogeographically, this area belongs to the Alpine Region and according to the Global Bioclimatic Classification System developed by Rivas-Martínez (2007), the bioclimate is temperate oceanic, with a mean annual temperature of 8°C, mean annual rainfall of 1,419 mm and a W-E continentality gradient. Long history of livestock and forest exploitation shaped the landscape of this area. Consequently, there is large landscape heterogeneity with semi-natural grasslands, scrublands, natural forests and *Pinus sylvestris* plantations.

The silver fir-beech forests of the area are included in the association *Scillo lilio- hyacinthi-Fagetum sylvaticae* Br.-Bl. ex O. Bolòs 1957, which encompasses omprophilous hyperhumid forests growing on calcareous bedrock (Rivas-Martínez et al., 1991). These forests do not show any clear management history, because of unsystematically conducted silvicultural practices with different intensities during the last century. In particular, the following silvicultural practices have been documented: group selection logging, shelterwood, selective logging system and exclusive fir exploitation.

2.2. Data collection

Silver fir-beech forests in an altitudinal range between 800 and 1,700 m a.s.l. were delimited using potential vegetation maps and aerial photographs provided by the Governments of Navarre and Aragón. North faced stands exceeding 30 ha were selected, out of which 14 stands were randomly chosen (Appendix A). Within each stand, four to five plots of 20 m x 20 m were randomly sampled, in total 68 plots. All sampling plots were located on an approximately 40 km long W-E direction. For each plot, the presence of vascular plant species (presence/absence data), light and climatic conditions, elevation, slope, coordinates and management category were recorded. Field sampling was conducted during the summer months of the years 2013 and 2014 with permits of the Governments of Navarre and Aragón.

Nomenclature follows *Flora iberica* (Castroviejo, 1986-2013), except for *Asteraceae, Geraniaceae* and *Poaceae*, which follow *Flora Europaea* (Tutin et al., 1968-1980).

Vascular plant species were sampled in three layers, but only herb layer species (including phanerophyte seedlings) were used in further analyses. Herb layer vascular plant species were categorised following Schmidt et al. (2011) on the basis of the information contained in the Vegetation-Plot Database of the University of the Basque Country (GIVD EU-00-011; Biurrun et al., 2012) and of the available reference lists about beech forest specialists (Willner et al., 2009). Four categories were distinguished: *Forest specialists* (FS), species largely restricted to closed forests; *Forest edge* (FE), species which prefer forest edges and clearings; *Generalists* (GS), which occur in forests as well as in open land, and *open area* (OA) species, which may occuroccasionally in the forest but prefer open lands (Appendix B).

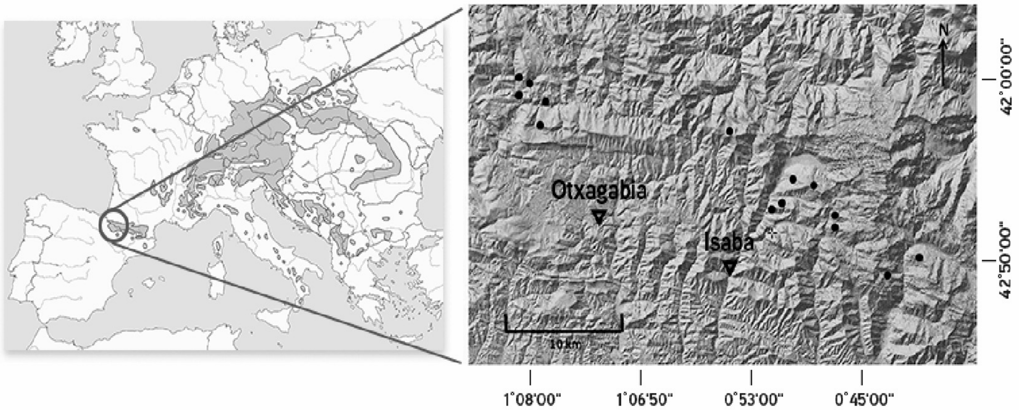

Fig. 1. *Abies alba* distribution (EUFORGEN 2009, www.euforgen.org, last accessed 20.5.2016) and location of the 14 sampled stands in the western Pyrenees, regions of Navarre and Aragón, northern Spain. The symbols representing the stands are not to scale in the figure.

Table 1. Climatic, topographic and light condition variables used in the analyses of species diversity in silver fir-beech forests in the western Pyrenees.

Variables	Range	Mean ± SD
Topography		
Elevation (m a.s.l.)	971-1651	1296 ± 179
Slope (%)	10-76	37.46 ± 16.63
Stand surface (ha)	30-93	55.91 ± 23.59
Light		
Transmission (%)	1.41-28.90	9.50 ± 4.38
Gaps (%)	0.95-25.40	5.25 ± 3.41
LAI	2.29-7.68	4.43 ± 1.11
Climate		
T Mean annual temperature (ºC)	7.20-10.80	8.74 ± 0.84
P Annual rainfall (mm)	1211-1601	1422 ± 71.36
It Thermicity index	64.40-182	113.5 ± 27.73
Ic Continentality index	15.14-17.62	16.25 ± 0.53
Io Ombrothermic index	11.67-15.44	13.52 ± 1.06

Variables of light conditions (Table 1) were obtained by hemispherical photography following VALERI design (Weiss et al., 2001). Nine photographs per plot were taken on the grid basis of 20 m x 20 m with a digital camera (Canon EOS 10D) and circular fish-eye lens (Sigma 8mm f/3.5 EX DG) mounted on a tripod 1 m above the ground. The camera was levelled and aligned to magnetic north. Due to sampling limitations our photography acquisitions were done in variable conditions, but mostly on cloudy days. The bias due to different time of image acquisition was considered minimal as there was no visible sunlight reflection in any photograph. Notes of slope inclination, altitude and coordinates were taken in each plot for the photography analysis. Before the photography analysis, camera was calibrated to define the optical centre and the projection function. Automatically exposed photographs were analysed by Hemisfer software version 2.12 (Schleppi et al., 2007). For photography analysis, five rings of 9° width were used, adapted for plot size and tree height. Only the blue band of the photographs was used to minimise the interference of multiple scattering in the canopy (Zhang et al., 2005) and to get the best contrast. Therefore, automatic threshold was applied (Nobis and Hunziker, 2005) with $\gamma = 2.2$. Considered variables were: *Transmission,* an overall canopy openness or total gap fraction within the defined rings which includes small and large gaps; *gaps,* the proportion of large gaps estimated according to Chen and Cihlar (1995), which corresponds to between-crown gaps, and LAI (Leaf Area Index) calculated by weighted ellipsoidal method (Thimonier et al., 2010), corrected for slope (Schleppi et al., 2007) and clumping index (Chen and Cihlar, 1995).

Climatic data (Table 1) were derived from digital maps (Ninyerola et al., 2005). Used variables were: mean annual temperature (T), annual rainfall (P) and three bioclimatic indexes (Rivas-Martínez, 2007): thermicity index ($It = (T+M+m) \times 10$; M: average maximum temperature of the coldest month of the year, m: average minimum temperature of the coldest month of the year), continentality index ($Ic = T_{max}-T_{min}$; T_{max}; mean temperature of the warmest month, T_{min}: mean temperature of the coldest month) and ombrothermic index ($Io = (Pp/Tp) \times 10$; Pp: yearly positive precipitation in mm, i.e. total average precipitation of those months with an average temperature higher than 0ºC, Tp: yearly positive temperature).

Management category for each plot was obtained combining data of time since last management activity, management type, tree age and presence of man-made stumps. Four management categories were established: *recently managed*, *long managed*, *recently abandoned* and *long abandoned*. Category *recently managed* corresponds to plots in which the last anthropogenic disturbance occurred approximately ten years ago, where no large trees can be found and management type applied was probably logging in group selection. Category *long managed* corresponds to plots in which logging occurred about 20 years ago, managed by shelterwood, group selection or single tree selection. Category *recently abandoned* corresponds to the plots without any management activities for more than 40 years but with visible man-made decaying stumps, rests of metal cables for wood extraction and abandoned skid roads. Management histories are different, in some cases without any data about it. Category *long abandoned* mostly belongs to the strict reserve Aztaparreta and some plots in inaccessible terrains with no evidence of logging, such as stumps presence for instance. Due to lack of data about the management practices in our study area, categorisation of plots to management categories was made by expert judgement.

2.3. Data analysis

2.3.1. General patterns

The percentage of occurrence of the herb layer species regarding habitat preference was calculated for the whole data set and for each management category separately. The differences among the management categories regarding the environmental variables were explored by non-parametric Kruskal-Wallis test and Mann-Whitney U test. Species richness variation among the management categories was computed as multiplicative beta diversity (Whittaker, 1960), simply expressed as $\beta = \gamma/\alpha$. Total number of species in the specified management category is represented by γ, and α is the mean number of species per plot within each management category. Taking into account that species richness is only one aspect of diversity, we adopted the terminology proposed by Tuomisto (2010), according to which, terms referring to alpha richness, beta richness and gamma richness are the appropriate terms when diversity is measured as species richness. Regarding gamma richness, sample-based rarefaction was performed to obtain the expected number of species for the same number of plots because of unbalanced number of plots among the management categories (Chao et al., 2014; Gotelli and Colwell, 2001). Interpolation and extrapolation sampling curves of species diversity were expressed by Hill numbers (Hill, 1973), where species richness corresponds to the diversity order of $q=0$. The analysis was performed with the *iNEXT* package in R.

2.3.2. Species richness

Generalized linear mixed models (GLMM) were used to determine the environmental variables that are driving the variation of species richness, following Bolker et al. (2009). We modelled total species richness, as well as richness partitioned for each species category except for *generalists,* due to the low number of species. Environmental variables were taken as fixed effects and stand was considered as a random effect. Poisson error distribution for count data and logarithmic link function were used. Backward-forward selection with AIC criteria was used to fit the most parsimonious model, and variables were scaled (zero mean, unit variance). Spearman correlation analysis among the explanatory variables was conducted in order to avoid collinearity. The model was fitted with function *glmer* from the *lme4* package. Management was a categorical variable and the level of *long abandoned* plots was set as a reference (model intercept), because forest ecosystems which have not been exposed to any direct or indirect human impact are preeminently suited for establishing reference conditions (Schmidt, 2005).

Additionally, post-hoc last-squares means test was used for pairwise comparisons between management categories, performed by *lsmeans* package. The goodness-of-fit of the model was expressed by pseudo-R^2 (Nakagawa and Schielzeth, 2013), calculated with *MuMIn* package in R. To assess the magnitude of the management effect we calculated the log response ratio, a suitable metric which expresses proportional differences in species richness between experimental and control stands. Log response ratio with corrected bias for small sample sizes (Hedges et al., 1999) was performed with *ARPobservation* package. Effect sizes of other variables were displayed using *effects* package.

2.3.3. Species composition

Relationships between species composition and environmental variables were explored by canonical correspondence analysis (CCA), combined with principal coordinates of neighbour matrices method (PCNM, Legendre and Legendre, 2012) to separate spatial effects from the effects of environmental factors in the variation partitioning because of local scale sampling and expected spatial effects. To obtain PCNM variables, we used geographical coordinates. Spatial data matrix was calculated with Euclidean distance measure. For creating truncate distance matrix, threshold distance was calculated to cover the nearest-neighbour of each plot. With adjusted distance matrix, principal coordinates analysis (PCoA) was run. Only significant axes ($p < 0.05$) obtained by false discovery rate for p-value correction (FDR, Verhoeven et al., 2005) from PCoA results were considered relevant for further analysis. Positive eigenvalues were used as a set of explanatory spatial variables in the partial CCA. Highly correlated variables were removed using variance inflation factor (VIF; all variables with values > 10 were removed; Borcard et al., 2011). Uncorrelated environmental variables were entered in the model, in which the significant ones were retained with forward selection (with criteria $p < 0.05$ level of significance).

To test differences in beta diversity among management categories, multivariate dispersion around group centroids method was applied (Anderson et al., 2006). This method measures beta diversity as an average dissimilarity of individual plots from their group centroid in multivariate space. Distances among plots were calculated by Sørensen dissimilarity measure. Plot dispersions were calculated as spatial median to their management category centroid. The permutation test for homogeneity of multivariate dispersions was performed with 9,999 permutations. The analysis was performed with *betadisper* function in *vegan* package in R. For the analyses on species composition and partial CCA, one plot was excluded because of its proximity to a stream, which could affect its species composition.

All the analyses were performed in R statistical environment, version 3.2.5 (R Foundation for Statistical Computing, Vienna, AT), except for partial CCA, for which CANOCO 5.1 (Ter Braak and Šmilauer, 2012) was used.

3. RESULTS

3.1. General floristic and environmental patterns

In the overall survey of 68 plots in the *Scillo-Fagetum* association, we identified 112 taxa (Appendix B). Mean species richness per plot was 14.69 ± 9.26, which varied from 3 to 44 species per plot. The most dominant tree species was *Fagus sylvatica*, followed by *Abies alba*; *Pinus sylvestris* and *Taxus baccata* occurred only occasionally. Shrub layer was not developed, except for *Fagus sylvatica* in juvenile phase appearing in the gaps and few occurrences of *Daphne laureola*. Herb layer was mainly formed by *forest specialists* (62%), with low abundances and pres-

Table 2. Distribution of species categories (FS, *forest specialists*; FE, *forest edge species*; GS, *generalists*; OA, *open area species*) regarding habitat preference across management categoriesin silver fir-beech forests in the western Pyrenees. Management categories: RM, recently managed, LM, long managed, RA, recently abandoned, LA, long abandoned.

Management category	Number of plots	Proportion of habitat preference species categories per management category (%)				Mean and st. dev. of habitat preference species categories per plot			
		FS	FE	GS	OA	FS	FE	GS	OA
RM	10	66.66	15.87	9.52	7.93	9.70±6.56	2.60±2.11	2.10±1.28	1.50±1.84
LM	28	62.63	14.28	5.49	17.58	11.21±5.87	3.60±2.42	2.78±0.99	1.53±3.14
RA	17	70.21	14.89	8.51	6.38	4.48±2.66	1.23±1.14	1.58±0.79	0.64±0.70
LA	13	76.08	13.04	2.17	8.69	7.20±3.19	2.46±2.02	2.00±1.00	0.76±0.59
Total	68	61.6	15.17	6.25	16.96	11.44±6.43	1.98±1.82	0.58±0.90	0.66±1.20

ence of *open area* species (17%) (Table 2). The most frequent species in the herb layer were: *Fagus sylvatica* seedlings (in 100% of the plots), *Carex sylvatica* (62%), *Dryopteris filix-mas* (62%), *Athyrium filix-femina* (57%), *Veronica montana* (52%) and *Oxalis acetosella* (50%). In the whole data set, 36 species (31%) occurred only once. As regards management categories, *long managed* forests contained the highest percentage of *open area* species and *long abandoned* forests the highest percentage of *forest specialists*. Table 2 shows the distribution of the four species categories on habitat preference across the management categories.

Climatic conditions varied over the sampled area along the 40 km transect, as shown in Table 1. According to the values of continentality index, the studied stands grow under oceanic climate (Ic range was from 15.14 to 17.62); most of them match the euoceanic subtype (Ic < 17),

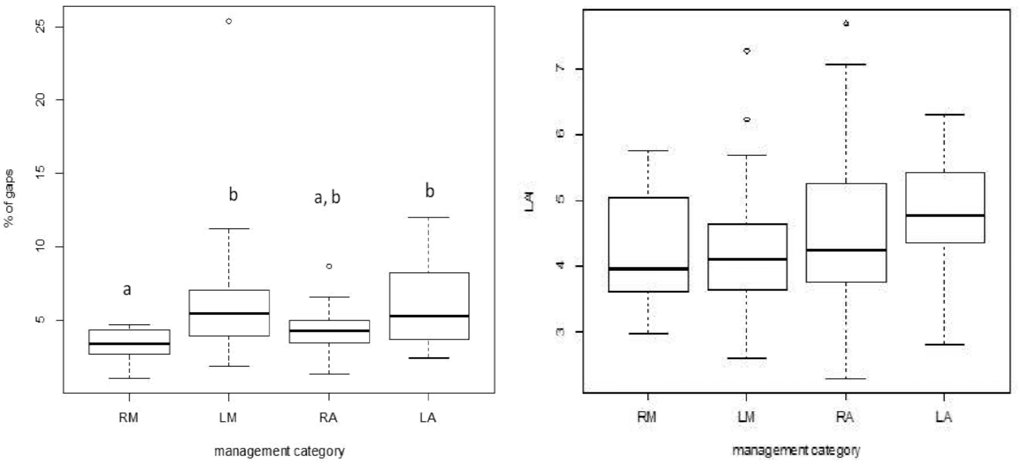

Fig. 2. Boxplots of *gaps* and LAI distribution by management category in silver fir-beech forests in the western Pyrenees. Empty circles represent outliers. The variable gaps differs amongmanagement categories at $p < 0.05$ level based on Kruskal-Wallis test (Chi-Squared = 14.95, $p = 0.002$). The variable LAI does notdiffer amongmanagement categories at $p < 0.05$ level based on Kruskal-Wallis test (Chi-Squared = 2.38, $p = 0.52$). Management categories: RM, recently managed, LM, long managed, RA, recently abandoned, LA, long abandoned.

Table 3. Alpha, beta and gamma richness relationship among the management categories in silver fir-beech forests in the western Pyrenees. Management categories: RM, recently managed, LM, long managed, RA, recently abandoned, LA, long abandoned.

Management category	Number of plots	Alpha richness	Beta richness	Gamma richness
RM	10	15.9 ± 10.56	3.96	63
LM	28	19.14 ± 9.80	4.75	91
RA	17	8.35 ± 4.62	5.62	47
LA	13	12.46 ± 5.36	3.69	46

but the two easternmost stands match the semi-continental subtype (Ic > 17). Ombrothermic index ranges from 11.67 to 15.44, distinguishing two types, humid (Io < 12) and hyperhumid (Io > 12). Only the two westernmost stands belong to the humid type.

Transmission and *gaps* were highly correlated (*r* = 0.91). For the whole data set, the average value of *transmission* was 9.43%, of which more than half is due to *gaps,* as the average value of *gaps* was 5.2%. The highest mean value of the variable *gaps* was found in *long managed* plots, where gaps were created by management practices and in *long abandoned* plots, where gaps were created by natural disturbances (Fig. 2). Besides, the ranges of values for the variable *gaps* were larger in *long managed* and *long abandoned* stands than in *recently managed* and *recently abandoned* stands (Fig. 2). LAI values showed high variability in all management categories. Although not significantly different, the highest median was found in *long abandoned* plots (Fig. 2). LAI and gaps were slightly correlated (*r* = -0.39) so we have included them separately in the GLMM analysis.

Recently abandoned plots showed the lowest alpha richness, albeit with the highest beta richness. Beta richness was lowest in *long abandoned* plots and alpha richness highest in *long*

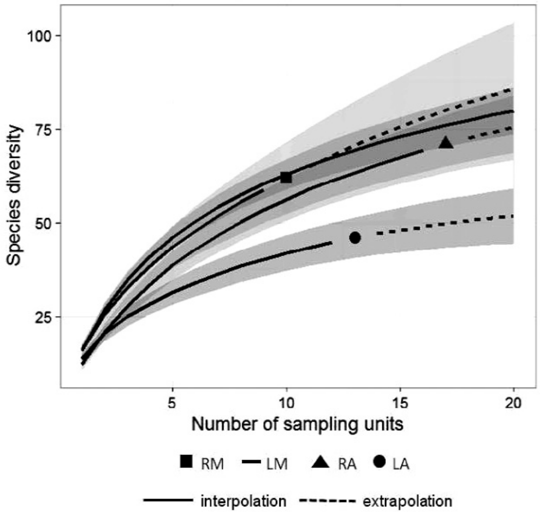

Fig. 3. Interpolation and extrapolation curves based on species richness (q = 0) for each management category in silver fir-beech forests in the western Pyrenees. Shaded area represents the bootstrap standard error and 95% confidence interval. Management categories: RM, recently managed, LM, long managed, RA, recently abandoned, LA, long abandoned.

managed plots (Table 3). Interpolation and extrapolation sampling curves showed that for the same minimum number of plots (10 plots precisely), species richness in *long abandoned* plots is lower than in *recently managed*, *long managed* and *recently abandoned* plots (Fig. 3).

3.2. Species richness

By modelling total species richness, three significant variables ($p < 0.05$) were retained: slope, management category and continentalityindex (Table 4). Species richness was negatively correlated with slope and positively correlated with continentality although the effects of these variables were weak. For a slope increase of 10% species richness decreased 3-9%, with stronger decrease in the steepest slopes, whereas for an Ic increase of 10%, it increased 2% (Fig. C.1 in Appendix C). Taking *long abandoned* category as a reference, management was significant only in the *recently abandoned* category, with a considerable species richness decrease of 40% (variance 0.03, CI: -0.76 to -0.04). In pairwise comparison of management categories significant differences (p < 0.05) were found between *long managed* with *recently managed* and *recently abandoned*. In the category *long managed* species richness increased 83% (variance 0.02, CI: -1.15 to -0.50) compared to *recently abandoned* category, whilst compared to *recently managed* category the increase was 20% (variance 0.05, CI: -0.68 to 0.29).

Slope and management category, level *recently abandoned,* were negatively correlated with FS richnes ($p < 0.05$) (Table C.1 in Appendix C). For a slope increase of 10% FS richness de-

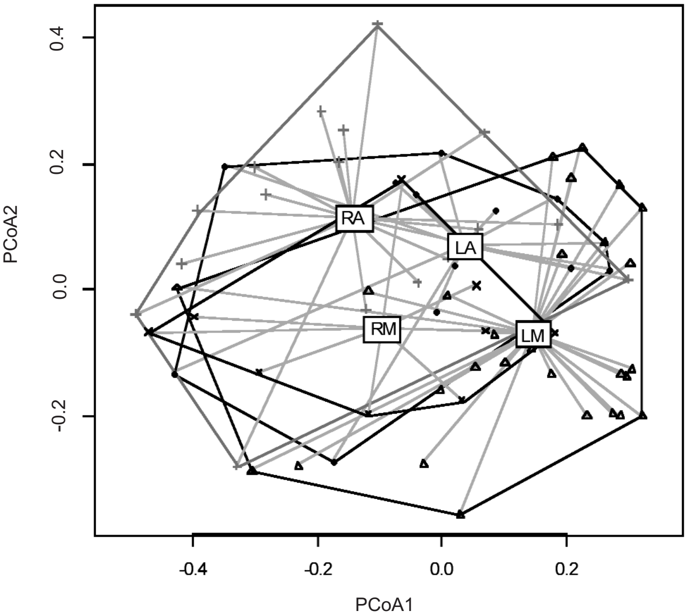

Fig. 4. Multivariate dispersion of plots around management category centroid in the multivariate space represented by PCoA 1 and PCoA 2 axes calculated on herb layer species composition of four management categories in silver fir-beech forests in the western Pyrenees. Plots dispersion is represented by grey lines; symbols represent centroids of management categories. The permutation test for homogeneity of multivariate dispersions did not show any clear evidence of different beta diversities among management categories (F = 2.29, Pr (> F) = 0.08). Management categories: RM, recently managed, LM, long managed, RA, recently abandoned, LA, long abandoned.

Table 4. Summary results of GLMMs explaining herb layer species richness in silver fir-beech forests in the western Pyrenees with respect to plot predictors of environmental variables. Poisson error distribution for count data and log link function were used. Stand was included as a random factor (random intercept). Management categories: RM, recently managed, LM, long managed, RA, recently abandoned, LA, long abandoned (model intercept).

Species richness ~ Slope + Ic + Management + (1 |stand)				
	Estimate	**Std. error**	**Z value**	**Pr (>|z|)**
(Intercept)	271.534	0.18925	14.348	< 2e-16***
Slope	-0.19563	0.05087	-3.846	0.00012 ***
Ic	0.17273	0.07311	2.363	0.01814*
Management: RA	-0.70325	0.21298	-3.302	0.00096***
Management: LM	0.244	0.18881	1.292	0.19625
Management: RM	-0.37119	0.23688	-1.567	0.11711

Table 5. Summary of the variation partitioning between the selected environmental variables and the spatial predictors of all data set, selected by the PCNM method. Fraction (a) and (b) represent unique contributions of each set of variables. Fraction (c) is their overlap.

Fraction	Variation (adj)	% of explained	% of all	DF	Mean Square
A	0.129	32.2	2.2	3	0.122
B	0.207	51.4	3.6	3	0.146
C	0.066	16.4	1.1	.	.
Total explained	0.402	100	7	6	0.148
All variation	5.765	.	100	66	.

creased 4-12%, with stronger decrease in the steepest slopes (Fig. C.2 in Appendix C). The effect of decreasing FS richness in *recently abandoned* plots comparing with the reference was similar as for total species richness. Precisely FS richness decreased 39% (variance 0.03, CI: -0.74 to -0.04). Comparing *long managed* with *recently abandoned* category we found exactly the same effect size as for total species richness (increase of 83%). Comparing the categories *long managed* and *recently managed* the effect was a bit weaker: in *long managed* category FS richness increased 16% (variance 0.05, CI: -0.62 to -0.29).

The model using FE richness as a response variable indicated three significant variables ($p < 0.05$). *Gaps* had a positive effect on FE richness, whereas slope and management, level *recently abandoned,* were negatively correlated (Table C.2. in Appendix C). For a gaps percentage increase of 10% FE richness increased 7-10%, with stronger increase in the highest gaps percentages. Slope effect also varied from 8 to 20%, with stronger FE richness decrease in the steepest slopes (Fig. C.3. in Appendix C). Although the model indicated differences between *recently abandoned* and *long abandoned* plots ($p = 0.03$), post hoc test did not show significant differences for the mentioned pair, nor for the rest of the pairs.

In the case of OA richness modelling the only one significant variable ($p< 0.05$) was *gaps* which had a positive moderate effect (Table C.3 in Appendix C). For a gaps percentage increase of 10% OA richness increased 15% (Fig. C.4 in Appendix C).

3.3. Herb layer species composition

PCNM analysis explained 7% of all variation (Table 5). Environmental variables that remained significant after forward selection were slope, ombrothermic index and management category, level *long managed*, and they explained 2.2% of total variation (fraction a). Spatial variables explained 3.6% of all variation, represented by three significant axes; PCO3, PCO10 and PCO11 (fraction b). Shared effect between environment and space contributed with 1.1% to total variation (fraction c). All fractions were highly significant ($p < 0.0001$).

The final model obtained by partial CCA, after removing spatial effects, explained 7% of the variation in species composition. All variance components were significant ($p < 0.05$), although the total amount of species compositional variation explained by the combined environmental variables was low. Downweighting of rare species or removing them did not improve the result.

Multivariate dispersion around group centroids analysis did not show any significant difference in beta diversity among the management categories (Fig. 4). Average distance to median was 0.41 for *recently managed* plots, 0.42 for *long managed* plots, 0.48 for *recently abandoned* plots and 0.39 for *long abandoned* plots. Pairwise differences were significant between *recently abandoned* and *long abandoned* plots ($p < 0.05$) and *recently abandoned* and *long managed* plots ($p < 0.05$)

4. DISCUSSION

4.1. General diversity patterns

The present work provides some insight into the patterns of species diversity in silver fir-beech forests in the western Pyrenees. Regardless of management type, stands of the studied association share main features with Central European beech forests, such as low species richness, low light levels, high competitive capacity of beech and strong litter accumulation (von Oheimb et al., 2005). These stands of the *Scillo-Fagetum* association contain European floristic elements (*Cardamine heptaphylla*, *C. pentaphyllos*, *Dryopteris filix-mas*, *Euphorbia amgydaloides*, *E. dulcis*, *Luzula sylvatica*, *Prenanthes purpurea*, *Viola reichenbachiana*, etc.) and taxa with the centre of distribution in the Pyrenees and the North of the Iberian Peninsula, such as *Conopodium pyrenaeum*, *Helleborus viridis* subsp. *occidentalis*, *Saxifraga hirsuta*, *Scilla lilio-hyacinthus* and *Scrophularia alpestris* (Willner et al*.,* 2009).

4.2. Drivers of herb layer species richness

The analysis of total species richness and partial richness of species groups lead to slightly different results. Management category, continentality and slope had a weak effect on total species richness, whilst *forest edge* and *open area* species richness also responded to the percentage of large gaps, with a moderate effect. These groups of species are characterized as light demanding species which are indicating disturbances in forest ecosystems (Schmidt et al., 2011), both natural (in *long abandoned* plots) (Kucbel et al., 2010) and anthropogenic (in *long managed* plots). This significant and positive effect of gaps on species richness has already been reported in beech forests (Naaf and Wulf, 2007).

The positive effect of increasing continentality in the herb layer species richness can be attributed to an increase in summer (July) temperatures, which had a larger range (11.62-18.02ºC) than winter (January) temperatures (-0.7-3.6ºC). Odland and Birks (1999) also found a positive relationship between mean July temperature and plant species richness for a similar altitudinal range (700-1500 m). Generally, a positive relationship between plant species richness and temperature was reported in several studies at regional scale (Austin et al., 1996; Wohlgemuth, 1998).

Leuschnerand Lendzion (2009) did not find significant differences on species richness among north-facing shallow and steep slopes in German beech forests. Nevertheless, it has to be considered that in this study slopes ranged between 14 and 28%, whereas in our study they ranged between 10 and 76%. The obtained results suggest that steep slopes play a role in species richness, leading to lower soil moisture or loss of nutrients (Chen et al., 2016). In fact, several studies concluded that in temperate forests, species richness increased with soil moisture (Härdtle et al., 2003; Gálhidy et al., 2006). The species richness decrease linked to steep slopes may also be caused by topsoil damage related to avalanche disturbances (Bebi et al., 2007).

As regards the effect of forest management on species richness, there is still no consensus weather unmanaged forests are more species rich than managed forests because of contrasting results obtained on the local scale (reviewed in Paillet et al., 2010). As different terminology is used to describe managed and unmanaged forests, the comparison of results obtained from local scale studies, which comprise different management types and histories, can be misleading. Whilst Burrascano et al. (2009) considered only old-growth forests as unmanaged, other studies also included in this category forests which had not been managed for at least 20 years (Paillet et al., 2010) or for the last few decades (Schmidt, 2005). In the present study we have established four management categories, of which *recently abandoned* and *long abandoned* could be considered as unmanaged forests for further comparisons.

According to our results, species richness decreases in *recently abandoned* plots, which is consistent with the results of several studies conducted in temperate forests (Schmidt, 2005; Sebastià et al., 2005; von Oheimb and Härdtle, 2009), although other studies reported that unmanaged forests contained more plant species than managed forests (Burrascano et al., 2009) or no difference in species richness (Bossuyt et al., 1999; Sitzia et al., 2012). Actually, the time since management abandonment is a crucial factor, because forest condition and structure are gradually changing over time (Fenton and Bergeron, 2008). Hence, the effect of management on the species richness varies depending on the time since management stops (Paillet et al., 2010). As the management categories considered in the present study partly represent the time since management abandonment, management effect (direction and effect sizes) differed. Precisely, the strongest effect (83%) on species richness decrease was detected in *recently abandoned* stands comparing to *long managed* ones, whichshow higher percentage of large gaps that remain since former intensive logging, and so they can host higher species richness. Approximately 40 years of management cessation leads to biomass accumulation with drastic canopy closure, which causes a decline of species richness (Heiri et al., 2009). Due to absence of logging and natural disturbances, beech proportion increasesbecause of high shade tolerance and competitive ability (Boch et al., 2013). The relevant increase (40%) of species richness in *long abandoned* category comparing with *recently abandoned* represents the gradual natural recovery of species richness. As the *long abandoned* stands correspond to more stable ecosystems with established natural dynamics, gaps created by natural disturbances permit higher species richness (Burrascano et al., 2013). Finally, the observed richness decrease (20%) in *recently managed* plots comparing to *long managed* plots could be associated with differences in forest structure and consequently light levels, as well as damaged soil structure due to recent logging (Honnay et al., 1999). The interaction of these factors could hamper higher species richness in *recently managed* stands.

Summarizing, the time since management abandonment plays a key role in species richness in silver fir-beech forests in western Pyrenees. In specific, recent abandonment of forest management considerably decreases species richness but our study did not confirm the differences between managed (*recently* and *long managed*) and unmanaged stands (*long abandoned*). Nevertheless, these results are context-sensitive above all to management history.

4.3. Herb layer species composition

Regarding variation partitioning analysis, space contributed more than environmental variables to explained variation, which indicates the existence of neutral processes and dispersal limitation (Peres-Neto et al., 2006). These results should be interpreted in terms of sampling scale, which plays a role determining spatial structuring of species, because different environmental factors affect species clustering at different spatial scales, as suggested by Chase (2014) and Garzon-Lopez et al. (2014). Plant communities are highly niche-structured at larger scales, and largely neutrally structured at smaller scales (Chase, 2014). Accordingly, our case study, conducted in one specific association, could correspond to a neutrally structured community because ecological gradients are weak at this spatial scale. Therefore, high spatial effect contribution in explained variation reflects strong evidence of neutral processes or neutrally structured communities (Chase, 2014). The spatial effect detected by PCNM analysis was related to broad and intermediate scale patterns. Species clustering, in our data, can have different origins. At first sight, spatial structuring could occur because of heterogeneous topography of the sampled area, formed by a mosaic of valleys and high peaks as natural barriers that could hamper seed dispersion. Lastly, it could also be attributed to unmeasured environmental variables such as soil properties and forest structure or to some past disturbance which we did not control. These variables could considerably reduce the contribution of space to explained variation (Chang et al., 2013). Data about landscape heterogeneity are lacking in our study, although they were found as important determinants in studies of species diversity (Zelený et al., 2010). Species spatial clustering caused by environmental factors or limited dispersal is still subject of research, due to difficulties in their differentiation (Wiegand et al*.,* 2007).

Species composition, after removing spatial effects, was driven by slope, ombrothermic index and management category (level long managed). Although several studies reported management effects on species composition (Wulf, 1997; Verheyen et al., 2003; Decocq et al., 2004), our analyses only explained a low percentage of variation by forest management. *Long managed* plots contributed the most to explained variation because of their different species composition; in particular, they showed the highest percentage of *open area* species associated with large gaps, such as *Atropa bella dona*, *Sambucus ebulus* and *Rubus* sp.pl. Much variation remained unexplained, which is a common result in the usage of ordination methods (Økland, 1999), and part of this variation can be attributed to a random stochastic component of the variation (Borcard and Legendre, 1994), because recorded species were scattered over the studied area, for instance *Taxus baccata, Conopodium pyrenaeum* and *Pyrola minor.* Sampling design on large areas assumes high variability in species composition with more rare species that could impute noise in the model (Cao et al., 2001).

Despite the difficulties in defining silvicultural practices in the context of type, intensity and frequency, our results suggest that species richness and species composition are affected by forest management. However, we did not find significant differences in beta diversity among management categories. As pairwise comparison on beta diversity showed significant differences between some management categories, these categories are reflecting a gradient across which species composition changes. Disturbances differ in their severity, frequency, duration, seasonality, spatial extent and other (Buhk et al., 2007), and established management categories summarised these notions. Nevertheless, we assume that our subjective classification could affect the results. Goebel and Hix (1997) and Motzkin et al. (1999) also noticed the problem of assessing studies about forest ecosystems when information of management practices is lacking.

5. CONCLUSIONS

We advocate that so far former management affects forest functioning and therefore species diversity. Our previous understanding of these forest ecosystems regarding management was scarce, so our study, covering large area of silver fir-beech forests, permitted us insight into the variety of management types used in these forests. High variety of management types and management histories is comprised under the term unmanaged forests in current literature, so any generalization of the results should be interpreted with care. Both the time since management abandonment and the management history are important issues because the restoration of natural dynamics is gradual and the overall ecosystem recovery is a long-term process (Paillet et al., 2015).

The present study focuses on vascular plant diversity in the Western Pyrenean silver fir-beech forests. Nevertheless, we are aware that other taxonomic groups such as bryophytes and lichens should also be addressed in further studies for a better understanding of the management effect on plant diversity.

ACKNOWLEDGEMENTS

We thank Daniel Garcia Magro for help with field work, Mercedes Herrera, Juan Antonio Campos, Diego Liendo, Francesco Sabatini, Sabina Burrascano, David Zelený, Francesco Chianucci and Patrik Schleppi for their valuable comments.

Funds from the project IT299-10 for research groups of the Basque Government have been used for this survey.

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SUPPORTING INFORMATION

APPENDIX A. Characteristics of the sampled stands in silver fir-beech forests in the western Pyrenees.

Stand	Elevation (m a.s.l.)	Stand's coordinates (x,y)	Surface (ha)
Lizardoia	980-1080	0653820, 4763330	49
San Fermin	1000-1230	0655930, 4761810	49
Eskalera	990-1140	0654482, 4760315	30
Iturtxarra	990-1100	0651107, 4760302	35
Burdinzkoa	1140-1230	0653604, 4759107	30
Pikatua	110-1300	0661514, 4758615	32
Maze	1320-1520	0677288, 4751014	68
Otsobieta	1300-1370	0676476, 4750586	32
Selva Grande	1250-1290	0676174, 4754505	81
Aztaparreta	1600-1650	0677940, 4753194	93
Gamueta	1340-1530	0679985, 4750580	82
Las Eras	1350-1420	0679594, 4749497	63
Selva de Oza	1200-1400	0686280, 4744519	32
Pavo	1390-1410	0690065, 4746704	73

APPENDIX B. Vascular plant species list in silver fir-beech forests in the western Pyrenees (FS, forest specialist; FE, forest edge species; GS, generalists; OA, open area species).

Plant Species	Family	Habitat	Frequency
Abies alba	Pinaceae	FS	56
Acer opalus	Aceraceae	FS	4
Adenostyles alliariae	Asteraceae	FE	13
Agrostis capillaris	Poaceae	OA	7
Ajuga reptans	Labiateae	GS	6
Alchemilla sp.	Rosaceae	OA	1
Anemone nemorosa	Ranunculaceae	FS	2
Asplenium trichomanes	Aspleniaceae	OA	1
Athyrium filix-femina	Athyriaceae	FS	39
Atropa bella donna	Solanaceae	FE	1
Blechnum spicant	Blechnaceae	FS	7
Brachypodium pinnatum subsp. *rupestre*	Poaceae	OA	7
Brachypodium sylvaticum subsp. *sylvaticum*	Poaceae	FS	6
Cardamine flexuosa	Brassicaceae	FS	28
Cardamine heptaphylla	Brassicaceae	FS	20
Cardamine impatiens subsp. *impatiens*	Brassicaceae	FS	1
Cardamine pentaphyllos	Brassicaceae	FS	5
Carex digitata	Cyperaceae	FS	3
Carex divulsa subsp. *divulsa*	Cyperaceae	OA	3
Carex leporina	Cyperaceae	OA	1
Carex muricata subsp. *pairae*	Cyperaceae	OA	1
Carex remota	Cyperaceae	FS	3
Carex sylvatica	Cyperaceae	FS	42
Cephalanthera damasonium	Orchidaceae	FS	1
Chrysosplenium oppositifolium	Saxifragaceae	FS	3
Circaea lutetiana subsp. *lutetiana*	Onagraceae	FS	3
Cirsium palustre	Asteraceae	OA	2
Conopodium pyrenaeum	Umbelliferae	FS	1
Cynosurus cristatus	Poaceae	OA	1
Daphne laureola	Thymelaeaceae	FS	9
Daphne mezereum	Thymelaeaceae	FS	1
Deschampsia flexuosa	Poaceae	GS	6
Digitalis purpurea	Scrophulariaceae	FE	1
Dryopteris affinis subsp. *affinis*	Aspidiaceae	FS	4
Dryopteris affinis subsp. *borreri*	Aspidiaceae	FS	5
Dryopteris dilatata	Aspidiaceae	FS	6
Dryopteris filix-mas	Aspidiaceae	FS	42
Epilobium montanum	Onagraceae	FS	15
Epipactis helleborine	Orchidaceae	FS	14
Epipactis microphylla	Orchidaceae	FS	1
Euphorbia amigdaloides	Euphorbiaceae	FS	15
Euphorbia dulcis	Euphorbiaceae	FS	1
Fagus sylvatica	Fagaceae	FS	68
Festuca rubra s.l.	Poaceae	GS	2
Fragaria vesca	Rosaceae	FE	17
Fraxinus excelsior	Oleaceae	FS	7
Galium odoratum	Rubiaceae	FS	19

APPENDIX B (Cont.).

Plant Species	Family	Habitat	Frequency
Galium rotundifolium	Rubiaceae	FS	1
Geranium robertianum	Rubiaceae	FE	19
Geum urbanum	Rosaceae	FE	1
Gymnocarpium dryopteris	Athyriaceae	FS	11
Hedera hélix	Araliaceae	FE	3
Helleborus viridis subsp. *occidentalis*	Ranunculaceae	FS	7
Hieracium murorum	Asteraceae	FS	3
Hordelymus europaeus	Poaceae	FS	18
Hypericum androsaemum	Guttiferae	FS	1
Ilex aquifolium	Aquifoliaceae	FS	6
Isopyrum thalictroides	Ranunculaceae	FS	2
Juncus effusus	Juncaceae	OA	3
Lamium galeobdolon	Labiateae	FS	19
Lapsana communis subsp. *communis*	Asteraceae	FE	1
Lathraea clandestina	Scrophulariaceae	FS	22
Luzula multiflora subsp. *congesta*	Juncaceae	FS	1
Luzula pilosa	Juncaceae	FS	3
Luzula sylvatica	Juncaceae	FS	15
Lysimachia nemorum	Primulaceae	FS	6
Meconopsis cámbrica	Papaveraceae	FE	3
Melica uniflora	Poaceae	FS	5
Milium effusum	Poaceae	FS	15
Moehringia trinervia	Caryophillaceae	FS	9
Monotropa hypopitys	Monotropaceae	FS	7
Mycelis muralis	Asteraceae	FS	5
Neottia nidus-avis	Orchidaceae	FS	18
Oxalis acetosella	Oxalidaceae	FS	34
Pinus sylvestris	Pinaceae	GS	4
Poa nemoralis	Poaceae	FS	5
Poa trivialis subsp. *feratiana*	Poaceae	OA	1
Polystichum aculeatum	Aspidiaceae	FS	33
Populus tremula	Salicaceae	FE	1
Potentilla sterilis	Rosaceae	FS	6
Prenanthes purpurea	Asteraceae	FS	1
Pteridium aquilinum subsp. *aquilinum*	Hypolepidaceae	OA	1
Pyrola minor	Pyrolaceae	FS	1
Quercus petraea	Fagaceae	FS	1
Ranunculus repens	Ranunculaceae	OA	1
Ranunculus tuberosus	Ranunculaceae	FS	1
Rosa arvensis	Rosaceae	FS	2
Rubus idaeus	Rosaceae	FE	5
Rubus sp.pl.	Rosaceae	GS	12
Salix caprea	Salicaceae	FE	7
Sambucus ebulus	Caprifoliaceae	OA	5
Sambucus racemosa	Caprifoliaceae	FE	1
Sanicula europea	Umbelliferae	FS	1
Saxifraga hirsuta subsp. *hirsuta*	Saxifragaceae	FS	17
Scilla lilio-hyacinthus	Liliceae	FS	5

APPENDIX B (Cont.).

Plant Species	Family	Habitat	Frequency
Scrophularia alpestris	Scrophulariaceae	FE	31
Sorbus aria	Rosaceae	FS	1
Sorbus aucuparia	Rosaceae	FE	27
Stellaria media	Caryophillaceae	OA	1
Taraxacum officinale	Asteraceae	OA	2
Taxus baccata	Taxaceae	FS	1
Tilia platyphyllos subsp. *platyphyllos*	Tiliaceae	FS	1
Tussilago fárfara	Asteraceae	OA	1
Ulmus glabra	Ulmaceae	FS	4
Urtica dioica	Urticaceae	OA	5
Vaccinium myrtillus	Ericaceae	FE	2
Veronica chamaedrys subsp. *chamaedrys*	Scrophulariaceae	GS	7
Veronica montana	Scrophulariaceae	FS	36
Veronica officinalis	Scrophulariaceae	GS	3
Veronica serpyllifolia	Scrophulariaceae	OA	1
Vicia sepium	Fabaceae	FE	2
Viola reichenbachiana	Violaceae	FS	23

APPENDIX C. Summary results of modelling herb layer species richness in silver fir-beech forests in the western Pyrenees with respect to environmental characteristics.

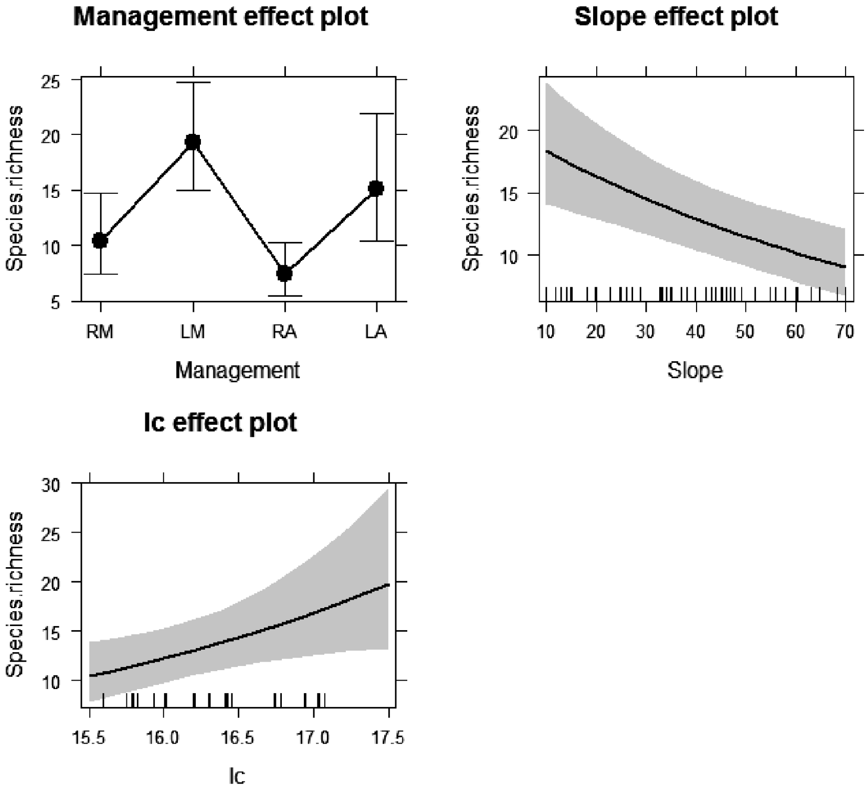

Fig. C.1. Model response of species richness to three significant variables (management, slope and continentality index) as predicted by GLMMs model, with 95% confidence intervals. Vertical axis is displayed on the scale of the response. Management categories: RM, recently managed; LM, long managed; RA, recently abandoned; LA, long abandoned.

Table C.1. Summary results of GLMMs explaining FS richness in silver fir-beech forests in the western Pyrenees with respect to plot predictors of environmental characteristics. Poisson error distribution for count data and log link function were used. Stand was included as a random factor (random intercept). Management categories: RM, recently managed; LM, long managed; RA, recently abandoned; LA, long abandoned.

	FS richness ~ Slope + Management + (1 |stand)			
	Estimate	**Std. error**	**Z value**	**Pr (>|z|)**
(Intercept)	217.407	0.21087	10.310	< 2e-16***
Slope	-0.15975	0.06315	-2.530	0.01141*
Management: RA	-0.65368	0.25066	-2.608	0.00911**
Management: LM	0.22602	0.2188	1.033	0.3016
Management: RM	-0.30998	0.27915	-1.110	0.26681

The model explained 33.59% of variation in species richness with fixed factors (marginal R^2) and 61.15% of variation with fixed and random factors (conditional R^2).

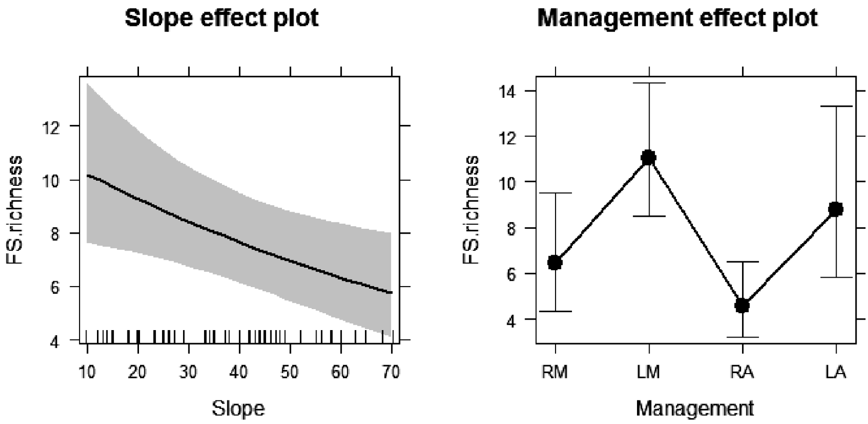

Fig. C.2. Model response of FS richness to two significant variables (management and slope) as predicted by GLMMs model, with 95% confidence intervals. Vertical axis is displayed on the scale of the response. Management categories: RM, recently managed; LM, long managed; RA, recently abandoned; LA, long abandoned.

Table C.2. Summary results of GLMMs explaining FE richness in silver fir-beech forests in the western Pyrenees with respect to plot predictors of environmental characteristics. Poisson error distribution for count data and log link function were used. Stand was included as a random factor (random intercept). Management categories: RM, recently managed; LM, long managed; RA, recently abandoned; LA, long abandoned.

FE richness ~ Slope + Ic + Management + (1 |stand)				
	Estimate	**Std. error**	**Z value**	**Pr (>|z|)**
(Intercept)	0.78518	0.257	3.055	0.00225**
Slope	-0.35558	0.10826	-3.285	0.00102**
Gaps	0.21595	0.07899	2.734	0.00626**
Management: RA	-0.82311	0.37943	-2.169	0.03006*
Management: LM	-0.08431	0.29354	-0.287	0.77395
Management: RM	-0.08673	0.44345	-0.196	0.84494

The model explained 34.00% of variation in species richness with fixed factors (marginal R^2) and 41.57% of variation with fixed and random factors (conditional R^2).

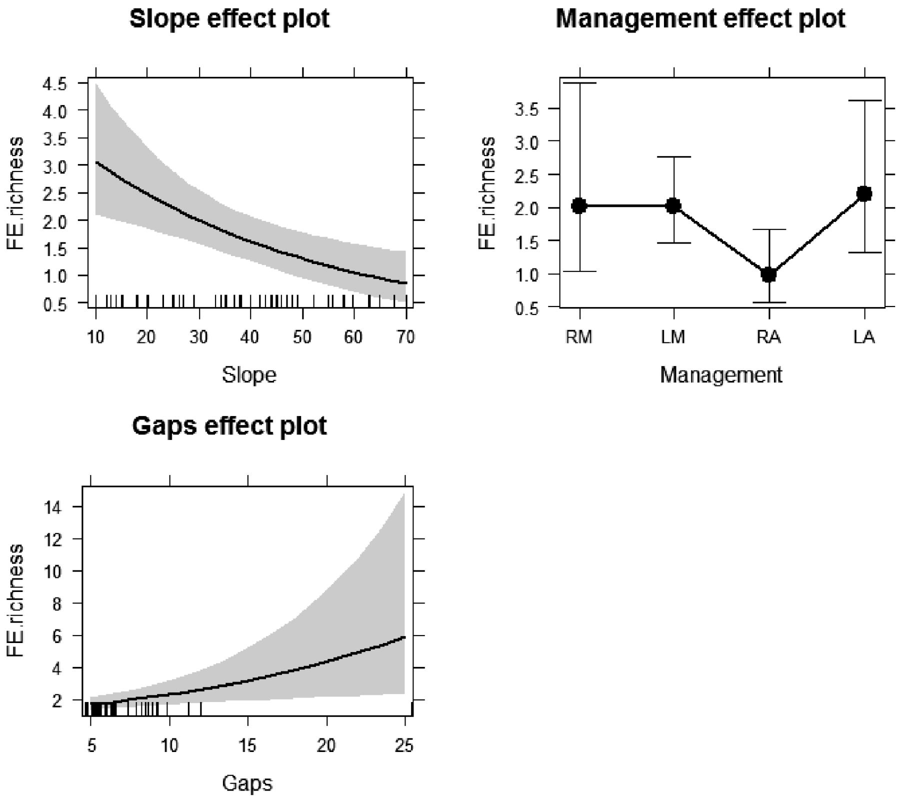

Fig. C.3. Model response of FE richness to three significant variables (management, gaps and slope) as predicted by GLMMs model, with 95% confidence intervals. Vertical axis is desplayed on the scale of the response. Management categories: RM, recently managed; LM, long managed; RA, recently abandoned; LA, long abandoned.

Table C.3. Summary results of GLMMs explaining OA species richness in silver fir-beech forests in the western Pyrenees with respect to plot predictors of environmental characteristics. Poisson error distribution for count data and log link function were used. Stand was included as a random factor (random intercept).

OA richness ~ Gaps + (1 |stand)				
	Estimate	**Std. error**	**Z value**	**Pr (>|z|)**
(Intercept)	-0.0308	0.20635	-0.149	0.881343
Gaps	0.30768	0.09022	3.410	0.00649***

The model explained 8.22% of variation in OA richness with fixed factors (marginal R^2) and 38.40% of variation with fixed and random factors (conditional R^2).

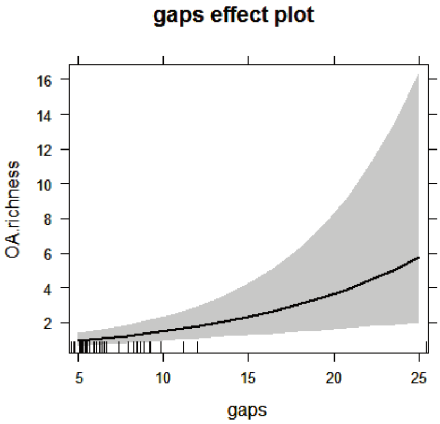

Fig. C.4. Model response of OA species richness to gaps as predicted by GLMMs model, with 95% confidence intervals. Vertical axis is desplayed on the scale of the response.

chapter 3

Vlatka Horvat (2018) PhD THESIS pp. 59-84

Intensive forest management affects bryophyte diversity in the western Pyrenean silver fir-beech forests

ABSTRACT

Understanding how bryophytes respond to management gradients in temperate forests is an important issue for their conservation and has major implications for forest management. This is especially true for western Pyrenean silver fir-beech forests, where high bryophyte turnover, as well as species loss, has been reported in the last 30 years. This study is the first to explore bryophyte diversity patterns across western Pyrenean silver fir-beech forests with different management intensities. Our specific aims were to determine the main drivers of bryophyte richness and turnover and explore which bryophyte species can be used as indicators of management intensity. The effect of management was assessed on the overall bryophyte diversity as well as on the bryophyte groups based on taxonomy, life cycle strategy, sensitivity to forest management intensity and habitat preference. Bryophyte diversity was analyzed by generalized linear mixed models and multiple regression analysis on distance matrices. The results suggest that bryophyte richness in the Pyrenean forests is decreasing with intensive forest management. The bryophyte richness decrease on highly disturbed stands can be attributed to a loss of suitable microhabitats, such as large trees. Elevational gradient, as a proxy of climatic factors, is also an important driver of bryophyte species richness in the studied area. Long-lived and epiphytic bryophytes decreased on steep slopes. Turnover was driven by elevation and percentage of large gaps, which might be linked with forest management. The results also suggest that Dierssen's classification of bryophytes regarding sensitivity to forest management is not suitable for the evaluation of the effects of forest management in the studied region. Our main recommendation for bryophyte conservation is to avoid intensive forest management and to minimize the forest practices in steep slopes which are prone to soil erosion.

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KEY WORDS **Bryophytes; Forest management intensity; Indicator species; Southwestern Europe; Species richness; Turnover**

PUBLISHED ***Biological Conservation* 215C, 81-91 (2017)**

ABBREVIATIONS AIC, Akaike Information Criterion; GLMM, Generalized Linear Mixed Model; LAI, Leaf Area Index; LCS, life cycle strategy; MRM, Multiple regression on distance matrices; SMI, bryophyte sensitivity to forest management.

1. INTRODUCTION

Non-vascular plants are an integral component of forest ecosystems and represent a significant part of plant species diversity (Lesica et al., 1991), although very often they are ignored in vegetation surveys (Bagella, 2014). Bryophytes support important ecosystem functions by increasing structural complexity and playing a role in nutrient cycles and moisture retention, providing habitat for other taxa (Jonsson et al., 2015). In spite of their importance, the overall knowledge about their role in ecosystems is still limited (Glime, 2013). In forest ecosystems, bryophytes affect soil thermal regimes (Glime, 2001), moisture (Fenton et al., 2006) and nutrient availability (Sveinbjörnsson and Oechel, 1992). Hitherto, it has been reported that at a coarse scale bryophyte assemblages in forest ecosystems are driven by climatic factors (Sun et al., 2013), but also by forest continuity (Frego, 2007), historical factors (Fritz and Brunet, 2010) and tree logging (Nelson and Halpern, 2005; Kantvilas et al., 2015). Climatic conditions, such as moisture, temperature and precipitation, strongly depend on the elevational gradient, which is consequently, an important driver of bryophyte diversity (Grau et al. 2007). Studies investigating the effect of elevation on bryophyte diversity generally agree that their relation is positive linear or humped shaped, depending on the longitude of the elevational gradient studied (Spitale et al., 2016). Topography is another important factor for bryophyte diversity (Bruun et al., 2006) determining the environmental heterogeneity and quantity of available niches in the sense of variety of micro-relief habitats. At a small scale, forest management may determine bryophyte diversity through its effects on tree species diversity, vertical structure, canopy closure, microclimate and dead wood availability (Peterken, 1996; Bengtsson et al., 2000; Paillet et al., 2010). Forest structure determines the light conditions, which strongly affect the bryophyte diversity (Márialigeti et al., 2009; Tinya et al., 2009; Tinya and Ódor, 2016), as well as microclimatic conditions which are of high importance for bryophytes (Király and Ódor, 2010). Therefore, understanding how bryophytes respond to management gradients in temperate forests is an important issue for their conservation and has important implications for forest management.

Bryophytes are considered good ecological indicators due to their sensitivity to environmental changes because of their specific characteristics such as lacking true roots and a waxy cuticle (Gignac, 2001). However, little is known about bryophytes as indicators of forest management. To date, most of the studies focused on the management effect on bryophytes have been conducted in boreal forests (Mills and Macdonald, 2004; Vellak and Ingerpuu, 2005; Jonsson et al., 2015), whilst this knowledge is scarcer in European temperate forests (Bardat and Aubert, 2007; Király and Ódor, 2010; Müller et al., 2015). Previous local studies, some of them focused on specific microhabitats such as dead wood (Müller et al., 2015) and large trees (Fritz et al., 2009) have given contrasting results (Vellak and Ingerpuu, 2005; Friedel et al., 2006), although a meta-analysis conducted in temperate forests showed that managed forests host lower bryophyte richness than unmanaged ones (Paillet et al., 2010). Bryophytes respond differently to forest management depending on their taxonomic group or ecological affinities. For instance, mosses and liverworts often respond differently to environmental changes (Kuglerová et al., 2016) and liverworts are considered more sensitive to forest management (Lesica et al., 1991; Fenton and Frego, 2005). It has also been suggested that certain bryophyte species are sensitive to human impact whilst others are tolerant (Dierssen, 2001). Additionally, bryophyte classification regarding life cycle strategy may be adequate to evaluate forest management; for instance, pioneer species can be indicators of disturbances because of their high dispersal capacities and tolerance to microclimatic changes (Heinken and Zippel, 2004) and their low frequency in undisturbed forests (Stewart and Mallik, 2006). Certain bryophyte species are able to grow on any substrate (soil, rocks, bark and dead wood) (Stokland et al., 2012), whilst some of them grow exclusively as epixylic or epiphytic and thus strongly depend on the quantity of available substrate. It has been reported that epixylic and epiphytic species are more abundant and diverse in unmanaged forests than managed ones (Lesica et al., 1991). Because of forest management effects, cryptogamic epiphytes are considered a threatened group in temperate forests (Paillet et al., 2010) and useful for the evaluation of the forest management impact.

In this context, our study assesses the impact of forest management on bryophyte diversity in silver fir-beech forests from the western Pyrenees. Historically, these forests have been subjected to intensive exploitation through animal husbandry and logging, but the intensity and periodicity of forest management are barely known as data about conducted silvicultural practices are lacking (Horvat et al., 2017). Forest biomass and cover strongly increased in the last 50 years due to abandonment of these traditional management activities (Vicente-Serrano et al., 2000), and currently some of these stands have been declared Natural Parks and Strict Reserves. To our knowledge, the impact of forest management on bryophyte diversity has not yet been assessed in the Pyrenean forests. Western Pyrenean bryophytes are documented and compiled in the Catalogues of bryophytes of Navarre (Ederra, 1985) and Aragón (Infante and Heras, 2008); hence these data can be used as a baseline for a study of management impacts. Although not tackled directly, the management issue is encompassed in a study on long-term changes in bryophyte diversity in the western Pyrenean beech forests (Delgado and Ederra, 2013), which reported high turnover as well as local extinction of several species between 1982 and 2010.

Given the above, this study strives to explore for the first time bryophyte diversity patterns across western Pyrenean silver fir-beech forests with different management intensities taking into account management history and type, forest age and time since management cessation. According to the available literature, we expected that in well preserved forests bryophyte richness would be higher and more sensitive bryophyte species would be found. Conversely, we expected that intensively managed stands would be poorer in species. Our specific aims were to determine (i) Which are the main drivers of bryophyte species richness and richness of their ecological groups: forest management or environmental factors? (ii) Which are the drivers of bryophyte turnover, and which is the relative contribution of geographical distance, forest management and environmental factors to this turnover? (iii) Which bryophyte species can be used as indicators of management intensity?

2. METHODS

2.1. Study area

The study area is located in the Spanish part of the western Pyrenees (Fig. 1), in the regions of Navarre and Aragón. The landscape is characterised by mountains and valleys with bedrock formed by limestone and marly flysch. Biogeographically this area belongs to the Alpine Region and according to the Global Bioclimatic Classification System developed by Rivas-Martínez (2007) the bioclimate is temperate oceanic, with a mean annual temperature of 8°C, mean annual rainfall of 1419 mm and a W-E continentality gradient. A long history of livestock and forest exploitation has shaped the landscape of this area, and consequently vegetation cover is a mosaic of forest fragments and pastures. The silver fir-beech forests of the area are included in the association *Scillo lilio-hyacinthi-Fagetum sylvaticae* Br.-Bl. ex O. Bolòs 1957 (here called *Scillo-Fagetum*), which encompasses ombrophilous hyperhumid forests growing on calcareous bedrock (Rivas-Martínez et al., 1991). Silvicultural practices of varying intensities were conducted without any thought of standardisation and thus there is no clear management history during the twentieth century. In particular, the following silvicultural practices have been documented: group selection logging, shelterwood, selective logging system and exclusive fir exploitation.

2.2. Data collection

Silver fir-beech forests in an altitudinal range between 800 and 1,700 m a.s.l. were delimited using potential vegetation maps and aerial photographs provided by the Governments of Navarre and Aragón. North facing stands exceeding 30 ha were selected, out of which 16 stands were randomly chosen (Appendix A). Within the chosen stands 20 m × 20 m plots were randomly sampled, the number of plots per stand varying from one to nine, depending on stand size and accessibility. In total 71 plots were surveyed, which were also used for a survey of vascular plants (Horvat et al., 2017). All sampling plots were located on an approximately 40 km long W-E direction. At plot level bryophyte species, light conditions, slope, coordinates (ED50) and management category were recorded. Field sampling was carried out during the summer months of the years 2013 and 2014 with permits of the Governments of Navarre and Aragón.

2.2.1. Bryophyte collection and classification

Within the selected plots bryophyte presence/absence was recorded. Bryophytes were collected from all kinds of available habitats (soil, rocks, bark of large and small trees and deadwood) as bryophyte diversity patterns are intimately linked to habitat heterogeneity (Newmaster et al., 2005). Due to the small bryophyte size sampling effort can influence the species richness estimates (Chen et al., 2015), thus sampling effort was similar in each plot in the terms of the time spent. Within each plot all the specimens recognized as morphologically different were kept in marked envelopes for further identification in the laboratory. Nomenclature follows Ros et al. (2013) for mosses and Ros et al. (2007) for liverworts. The specimens were identified at species level, except some specimens of the genera *Grimmia*, *Schistidium* and *Ulota*. For the latter, only specimens with a developed capsule were identified at species level, the rest were identified at genus level, which occurred in 28 plots. Hence, to describe

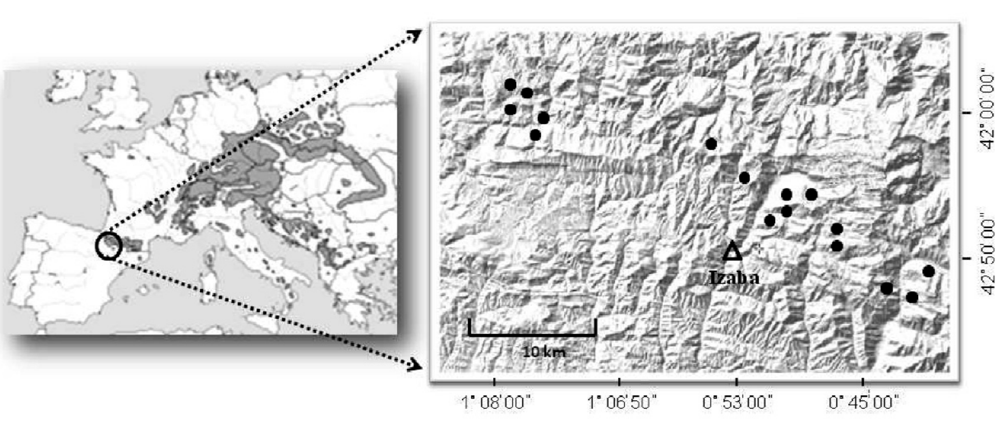

Fig. 1. *Abies alba* distribution (EUFORGEN 2009, www.euforgen.org, last accessed 20.5.2016) and location of the 16 sampled stands in the western Pyrenees, regions of Navarre and Aragón, northern Spain.

general floristic patterns we used species level (*Ulota crispa, U. bruchii* and *U. crispula*) and for the rest of analyses we used genus level.

In order to assess the impact of forest management, the bryophytes were grouped according to their taxonomy (mosses and liverworts), as well as their sensitivity to forest management intensity (SMI), their life cycle strategy (LCS) and substrate preference (epiphytes, epixylics, epilithic, terricolous and opportunistic). As regards SMI, we applied the classification given by Dierssen (2001), which distinguished five categories: species occurring in habitats where human impact is absent (1), weak (2), moderate (3), strong (4) and very strong (5). As each species has been associated with one, two or three consecutive categories, we modified them into the following three: *sensitive,* for species occurring in habitats in which human impact was absent and weak, *moderately sensitive* for those occurring in habitats in which human impact was moderate, and *tolerant* for those occurring in habitats in which human impact was strong or very strong. The species not classified by Dierssen (2001) were evaluated according to the available literature. As an example, *Antitrichia curtipendula* was classified as *sensitive* because it has been reported in old-growth stands from western Oregon (Rosso et al., 2001). Although categorized as a vulnerable species (Garilleti and Albertos, 2012), *Orthotrichum shawii* was classifiedas *moderately sensitive* because it can occur in managed stands (Infante and Heras, 2008; Mazimpaka et al., 2012).

Regarding life cycle strategy (LCS), we followed Dierssen (2001), based on During (1979). We distinguished two categories, *short-lived* and *long-lived* bryophytes. The term *short-lived* refers to fugitives, annual shuttles, colonists, ephemeral colonists, pioneer colonists, short-lived shuttles and geophytes, whilst the term *long-lived* refers to long-lived shuttles, competitive perennials, stress tolerant perennials and dominant perennials. Finally, species were classified as epixylic, epiphytic, epilithic, terricolous and opportunistic (occurring on many substrates such as rock-bark, bark-dead wood, dead wood-soil etc.) following the classification of Heilmann-Clausen et al. (2014). For the species not enhanced by Heilmann-Clausen et al. (2014) we used the classification proposed by Dierssen (2001).

Specimens identified to the genus level, e.g. *Grimmia* and *Schistidium,* were taken into account only for the taxonomic classification.

2.2.2. Environmental variables

Variables of light conditions (Table 1) were obtained by hemispherical photography following VALERI design (Weiss et al., 2001). Nine photographs per plot were taken on the grid basis of 20 m × 20 m with a digital camera (Canon EOS 10D) and circular fish-eye lens (Sigma 8mm f/3.5 EX DG) mounted on a tripod 1 m above the ground. The camera was levelled and aligned to magnetic north. Due to sampling limitations our photography acquisitions were done in variable conditions, but mostly on cloudy days. The bias due to different time of image acquisition was considered minimal as there was no visible sunlight reflection in any photograph. Notes of slope inclination, altitude and coordinates were taken in each plot for the photography analysis. Before the photography analysis, the camera was calibrated to define the optical centre and the projection function. Automatically exposed photographs were analysed by Hemisfer software version 2.12 (Schleppi et al., 2007). For photography analysis, five rings of 9° width were used, adapted for plot size and tree height. Only the blue band of the photographs was used to minimise the interference of multiple scattering in the canopy (Zhang et al., 2005) and to get the best contrast. Therefore, automatic threshold was applied (Nobis and Hunziker, 2005) with $\gamma = 2.2$. Considered variables were: *Transmission,* an overall canopy openness or total gap fraction within the defined rings which includes small and large gaps; *gaps,*

Table 1. Climatic, topographic and light condition variables used in the analyses of bryophyte diversity in silver fir-beech forests in the western Pyrenees.

Variables	Range	Mean ± SD
Topography		
Elevation (m a.s.l.)	971-1651	1296 ± 175.48
Slope (%)	10-76	36.8 ± 16.61
Stand surface area (ha)	30-93	56.52 ± 22.99
Light		
Transmission (%)	1.49-28.90	9.51 ± 4.31
Gaps (%)	0.95-25.40	5.28 ± 3.36
LAI	2.29-7.68	4.42 ± 1.10
Climate		
T Mean annual temperature (ºC)	7.20-10.8	8.70 ± 0.85
P Annual rainfall (mm)	1211-1601	1420 ± 71.32
It Thermicity index	64.4-182	112.2 ± 27.87
Ic Continentality index	15.14-17.62	16.27 ± 0.54
Io Ombrothermic index	11.67-15.44	13.55 ± 1.06

the proportion of large gaps estimated according to Chen and Cihlar (1995), which corresponds to between-crown gaps, and LAI (Leaf Area Index) calculated by weighted ellipsoidal method (Thimonier et al., 2010), corrected for slope (Schleppi et al., 2007) and clumping index (Chen and Cihlar, 1995).

Climatic data (Table 1) were derived from digital maps (Ninyerola et al., 2005). Used variables were: mean annual temperature (T), annual rainfall (P) and three bioclimatic indexes (Rivas-Martínez, 2007): thermicity index (It = $(T+M+m) \times 10$, where M: average maximum temperature of the coldest month of the year, and m: average minimum temperature of the coldest month of the year); continentality index (Ic = $T_{max}-T_{min}$, where T_{max}: mean temperature of the warmest month, T_{min}: mean temperature of the coldest month) and ombrothermic index (Io = (Pp/Tp) x 10, where Pp: yearly positive precipitation in mm, i.e. total average precipitation of those months with an average temperature higher than 0ºC, and Tp: yearly positive temperature). These bioclimatic indices, as a combination of simple climatic variables, have been frequently used in studies on plant communities (Biurrun et al., 2016); therefore we have also used them in our study. Management intensity for each plot was evaluated combining data of time since last anthropogenic disturbance, management type, stand age and presence of man-made stumps. Following these criteria, three categories of management intensity were established: *high*, *moderate* and *low*. Category *high* corresponds to plots in which the last disturbance occurred approximately ten years ago or less, no large trees can be found and management type applied was probably group selection or logging oriented towards large fir trees in the recent past. Category *moderate* corresponds to plots in which logging occurred about 20 years ago, managed by shelterwood, group selection or single tree selection. Category *low* corresponds to plots without any management activities for more than 40 years, but with different management histories, in some cases without any data about it. Plots included in this category belong mainly to forest reserves. Due to the lack of data about the management practices in our study area, categorisation of the plots to management categories was made by expert judgement.

For each stand we recorded geographical coordinates, elevation and stand surface area (Appendix A).

2.3. Data analysis

2.3.1. Data exploration

Bryophyte occurrence was calculated for the whole data set and for each management category separately. Sampling method accuracy was assessed using sample-based rarefaction to obtain the expected number of species for the same number of plots due to the unbalanced number of plots among the different management categories (Chao et al., 2014). Interpolation and extrapolation sampling curves of species diversity were expressed by Hill numbers (Hill, 1973), in which species richness corresponds to the diversity order of $q = 0$. The analysis was performed using *iNEXT* function from the *iNEXT* package in R. The differences among the management categories regarding the environmental variables were explored by boxplots.

2.3.2. Species richness

Generalized linear mixed models were used to determine the environmental variables that drive species richness. Total species richness, as well as richness of bryophyte groups (taxonomic, SMI, LCS and substrate preference) was modelled. Environmental variables were taken as fixed effects and stand was considered as a random effect. Poisson error distribution for count data and logarithmic link function were used. Backward selection with AIC criteria was used to fit the most parsimonious model. Spearman correlation analysis among the explanatory variables was conducted to avoid collinearity and all the variables were scaled (zero mean, unit variance). The model was fitted with function *glmer* from the *lme4* package in R. Since we hypothesized that elevation and management categories were correlated we included their interaction in the model.

Management was a categorical variable and the level *moderate* was set as a baseline (model intercept). Additionally, post-hoc last-squares means test was used for pairwise comparisons between management categories, performed by the *lsmeans* package in R. To assess the magnitude of the management effect the log response ratio was calculated; this is a suitable metric which expresses proportional differences in species richness between management categories. Log response ratio with corrected bias for small sample sizes (Hedges et al., 1999) was performed with *ARPobservation* package in R. The goodness-of-fit of the model was expressed by pseudo-R^2 (Nakagawa and Schielzeth, 2013), calculated with *MuMIn* package in R. Effect sizes were displayed using the *effects* package in R.

2.3.3. Species turnover

Species turnover was considered as the proportion of species composition that changes among sampling units (*sensu* Tuomisto in, Tuomisto 2010a,b). To quantify the variation explained by each variable and their shared effect on species turnover a distance-based variation partitioning approach was taken. This was done both because pairwise dissimilarity indices provide a natural measure for species turnover, and because a distance-based approach allows incorporating the effect of geographical distances into the models, as we were dealing with spatially clustered plots. By variation partitioning, we quantified the contribution of environmental differences and geographical distances to species turnover, which helps to separate between the effects of dispersal limitation and species responses to spatially autocorrelated environmental variables (Tuomisto and Ruokolainen, 2005; Lichstein, 2007; Sabatini et al., 2014). The response variable, species composition variation, was calculated using Sørensen dissimilarity measure. For each explanatory variable the corresponding dissimilarity matrix was created using the Euclidean distance. Management intensity was an ordinal variable with three levels: 1 for the category *low*, 2 for the category *moderate* and 3 for the category *high*.

The matrix of geographical distances was a matrix of linear spatial distances. Firstly, for each dissimilarity matrix a Mantel test (999 permutations) was run to select significant ones. All significant dissimilarity matrices in the Mantel test were used in a Multiple Regression on Distance Matrices analysis (MRM, Lichstein, 2007). Through backward elimination all non-significant matrices were dropped and the full MRM model obtained was used to quantify the variation explained by each variable, their unique and shared effect. As response matrices we used dissimilarity matrices based on the composition of all bryophyte species and additionally, of mosses, *moderately sensitive* bryophytes and *long-lived* bryophytes. No analysis was performed for liverworts, *sensitive, tolerant* and *short-lived* bryophytes because of the low number of species and their absence in several plots.

Additionally, an indicator species analysis (IndVal, Dufrêne and Legendre, 1997) was conducted to assess the affinity of bryophyte species for the categories of management intensity.

The analysis was performed with *ecodist* and *vegan* packages in R. All analyses were run using (v. 3.2-5) R statistical environment (R Foundation for Statistical Computing, Vienna, AT), except indicator species analysis, which was performed using the Ginkgo program (De Caceres et al., 2007).

3. RESULTS

3.1. General floristic and environmental patterns

In the overall survey of 71 plots inthe *Scillo-Fagetum* association, 88 bryophyte taxa were recorded: 75 mosses and 13 liverworts (Appendix B). The most frequent species were *Brachythecium velutinum* var. *velutinum* (found in 66% of the plots), *Pterigynandrum filiforme* var. *filiforme* (65%), *Isothecium alopecuroides* (60%) and *Hypnum cupressiforme* var. *cupressiforme* (49%). Twenty-three species occurred only in one plot (25% of collected bryophytes).

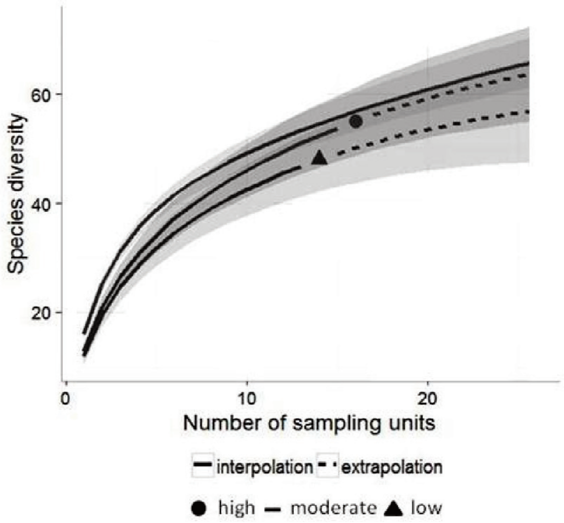

Fig. 2. Interpolation and extrapolation curves based on bryophyte species richness (q = 0) for each category of management intensity in silver fir-beech forests in the western Pyrenees. Shaded area represents the bootstrap standard error and 95% confidence interval. The categories of management intensity are *high*, *moderate* and *low*.

Table 2. Mean species richness of all bryophytes and their groups in the categories of management intensity (*high*, *moderate* and *low*) in silver fir-beech forests from the western Pyrenees.

	Management category			
	High	***Moderate***	***Low***	**All plots**
Number of plots	16	41	14	71
All bryophytes	12.81±6.83	16.00±6.41	11.87±5.00	14.36±6.46
Liverworts	1.93±1.61	2.90±2.03	2.28±1.54	2.09±1.88
Mosses	10.62±5.43	13.00±5.01	9.57±4.48	11.78±5.15
Sensitive	3.00±1.50	2.73±1.54	2.77±0.92	2.78±1.42
Moderately sensitive	5.37±3.18	7.14±3.53	4.53±2.75	6.22±3.44
Tolerant	4.43±3.44	6.02±2.62	4.61±2.69	5.39±2.87
Short-lived	3.50±2.85	3.75±1.94	2.53±1.85	3.45±2.17
Long-lived	9.31±4.60	12.14±5.22	9.38±3.75	10.95±4.95
Epilithic	1.5±2.03	2.02±1.73	1.14±1.35	1.73±1.75
Epiphytic	5.68±3.70	7.09±3.38	5.85±2.59	6.53±3.34
Epixylic	0.68±1.25	0.60±0.83	0.57±0.85	0.61±0.93
Opportunistic	3.06±1.76	3.80±1.83	2.71±1.43	3.42±1.79
Terricolous	1.87±1.31	2.36±1.90	1.57±1.82	2.09±1.78

Some of these species occurring only once are protected species such as *Buxbaumia viridis* and *Orthotrichum shawii,* which are included in the Red List of Spanish bryophytes categorized as "Vulnerable" (Garilleti and Albertos, 2012) and rare species as *Dicranodontium denudatum* and *Serpoleskea confervoides*.

The highest number of species was found in the *moderate* category of management intensity (Table 2). However, rarefaction curves indicate that species richness was generally similar among the three categories (Fig. 2), if a common test area is underlain.

As regards SMI, most of the species were classified as *moderately sensitive* (52%), followed by *tolerant* (31%) and *sensitive* species (17%) (Appendix B). Regarding LCS, 65% of the species were classified as *long-lived* species. With respect to substrate preference, 30% of the species found were epiphytic species, 26% epilithic, 17% terricolous, 19% opportunistic and 7% epixylic species (Appendix B). Mean species richness for the whole data set was 14 ± 6 per plot, whilst species richness average among management categories varied slightly. The mean richness of *sensitive* species per plot was surprisingly similar among management categories (Table 2).

Climatic conditions vary over the sampled area along the 40 km transect (Table 1). According to the values of the continentality index, the studied stands grow under oceanic climate (Ic from 15.14 to 17.62); most of them match the euoceanic subtype (Ic < 17), but the two easternmost stands match the semi-continental subtype (Ic > 17). The ombrothermic index ranges from 11.67 to 15.44, distinguishing two types, humid (Io < 12) and hyperhumid (Io > 12). Only the two westernmost stands belong to the humid type. Climatic variables, except annual rainfall, were correlated with elevation and between each other; for instance elevation with thermicity index (r = -0.85), continentality index (r = 0.70) and ombrothermic index (r = 0.68). Management categories differed regarding elevation and stand surface area as plots assigned to category *low* were located in higher elevations and had greater stand surface area (Fig. 3).

Regarding light conditions, *transmission* and *gaps* were highly correlated (r = 0.91). For the whole data set, the average value of *transmission* was 9.51%, of which more than half is due to *gaps,* as the average value of *gaps* was 5.28%.

3.2. Drivers of bryophyte richness

When modelling total bryophyte richness elevation and its interaction with management intensity were retained as significant variables ($p < 0.05$). The bryophyte richness decreased with increasing elevation (Table 3). However, the effect of elevation was dependent on the category of management intensity (interaction effect; Fig. 4). The number of species decreased with increasing elevation when the management intensity was *moderate* or *low*, but elevation did not affect species richness in the management category *high*. Differences between the *high*

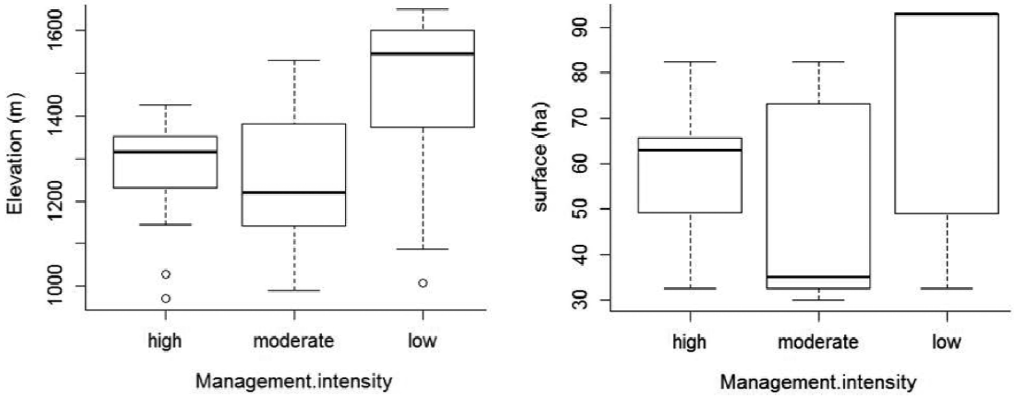

Fig. 3. Boxplots for elevation and stand surface area regarding management categories in silver fir-beech forests from the western Pyrenees.

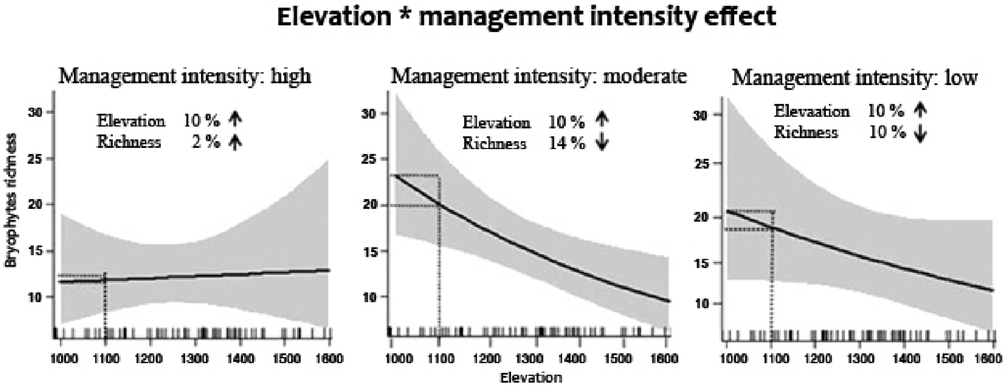

Fig. 4. Model response of bryophyte richness to interaction of elevation and management intensity variables as predicted by GLMMs model, with 95% confidence intervals. Vertical axis is displayed on the scale of the response. Management intensity: *high*, *moderate* and *low*. Effect of elevation on bryophyte richness differed among management categories; for the elevation increase of 10% (from 1000 to 1110 m), bryophyte richness increased 2% (from 11.6 to 11.8) in the management category *high*, whilst in the management categories *moderate* and *high* decreased 14% (from 23.3 to 20 species) and 10 % (19.5 to 17.7 species), respectively.

Table 3. Summary results of GLMMs explaining bryophyte richness with respect to plot predictors (Bryophyte richness ~ elevation + elevation*management + (1 | stand). Poisson error distribution for count data and log link function were used. Stand was included as a random factor. Management was a categorical variable and the level *moderate* was set as a baseline (model intercept). *$p < 0.05$, **$p < 0.01$ and ***$p < 0.001$.

Bryophyte richness ~ elevation + elevation*management + (1 | stand)				
	Estimate	**Std. error**	**Z value**	**Pr (>|z|)**
(intercept)	270.268	0.10684	25.29	< 2e-16***
Elevation	-0.26261	0.09419	-2.788	0.0053**
Elevation*management: *low*	0.09431	0.12833	0.735	0.4624
Elevation*management: *high*	0.29412	0.14956	1.967	0.0492*

Table 4. Summary results of GLMMs explaining liverwort and moss richness with respect to plot predictors (Liverwort richness ~ elevation + slope + (1| stand) and Moss richness ~ elevation + (1| stand), respectively). Poisson error distribution for count data and log link function were used. Stand was included as a random factor. Management was a categorical variable and the level *moderate* was set as a baseline (model intercept). * $p < 0.05$, ** $p < 0.01$ and *** $p< 0.001$.

Liverwort richness ~ elevation + slope + (1| stand)				
	Estimate	**Std. error**	**Z value**	**Pr (>|z|)**
(intercept)	0.63987	0.10168	6.296	3.11e-1***
Elevation	-0.28923	0.09449	-3.061	0.00221**
Slope	-0.31005	0.10384	-2.986	0.00283**

Moss richness ~ elevation + (1| stand)				
	Estimate	**Std. error**	**Z value**	**Pr (>|z|)**
(intercept)	251.218	0.09148	27.461	<2e-16***
Elevation	-0.16194	0.08046	-2.013	0.042*

and *moderate* categories were confirmed with a post hoc test. In the category *high*, species richness decreased for 22% (variance 0.02, CI: -0.51 to 0.05) comparing to the category *moderate* (Fig. 4). For an increase in elevation of 10%, species richness decreased approximately 10% (Fig. 4). The model explained 21.63 % of variation in species richness with fixed factors (marginal R^2) and 72.31 % of variation with fixed and random factors (conditional R^2).

When modelling bryophyte richness regarding their taxonomy, liverwort richness responded to elevation and slope, whilst moss richness responded to elevation. In both models the variables elevation and slope were negatively correlated (Table 4).

As regards SMI classification, *sensitive* bryophyte richness responded to slope and elevation, which had negative effect and to the interaction of elevation and management intensity. *Moderately sensitive* species richness responded negatively to elevation, whilst *tolerant* species richness responded negatively to slope (Table 5).

As regards LCS classification, *short-lived* species richness did not respond to any variable, whilst *long-lived* species richness responded negatively to elevation and slope and also to the interaction of management and elevation (Table 6).

Regarding substrate preference, terricolous bryophyte richness was negatively correlated with elevation and epiphytic bryophyte richness was negatively correlated with slope. Epilithic and

Table 5. Summary results of GLMMs explaining *sensitive* (*Sensitive* bryophyte richness ~ elevation + slope + elevation*management + (1| stand), *moderately sensitive* (*Moderately sensitive* bryophyte richness ~ elevation + (1| stand)) and tolerant bryophyte richness (*Tolerant* bryophyte richness ~ slope + (1| stand)) with respect to plot predictors. Poisson error distribution for count data and log link function were used. Stand was included as a random factor. Management was a categorical variable and the level *moderate* was set as a baseline (model intercept). * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$.

***Sensitive* bryophyte richness ~ elevation + slope + elevation*management + (1| stand)**

	Estimate	**Std. error**	**Z value**	**Pr (>|z|)**
(intercept)	0.86308	0.11115	7.765	8.17e-15***
Slope	-0.2027	0.07905	-2.564	0.0103*
Elevation	-0.2872	0.11708	-2.564	0.0103*
Elevation*management: *high*	0.75288	0.30851	2.440	0.0147*
Elevation*management: *low*	0.19496	0.186	1.048	0.2946

***Moderately sensitive* bryophyte richness ~ elevation + (1| stand)**

	Estimate	**Std. error**	**Z value**	**Pr (>|z|)**
(intercept)	17.792	0.0911	19.530	<2e-16***
Elevation	-0.3129	0.088	-3.555	0.001***

***Tolerant* bryophyte richness ~ slope + (1| stand)**

	Estimate	**Std. error**	**Z value**	**Pr (>|z|)**
(intercept)	16.656	0.0866	19.222	<2e-16***
Slope	-0.1878	0.0746	-2.517	0.012*

Table 6. Summary results of GLMMs explaining *long-lived* bryophyte richness (*Long-lived* bryophyte richness ~ elevation + slope + elevation * management + (1 | stand)) with respect to plot predictors. Poisson error distribution for count data and log link function were used. Stand was included as a random factor. Management was a categorical variable and the level moderate was set as a baseline (model intercept). * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$.

***Long-lived* bryophyte richness ~ elevation + slope + elevation * management + (1 | stand)**

	Estimate	**Std. error**	**Z value**	**Pr (>|z|)**
(intercept)	235.047	0.09152	25.684	< 2e-16***
Elevation	-0.35447	0.09031	-3.925	8.67e-05***
Slope	-0.11032	0.05531	-1.994	0.0461*
Elevation*management: *high*	0.3306	0.15832	2.088	0.0368*
Elevation*management: *low*	0.24014	0.13453	1.785	0.0743

opportunistic bryophyte richness did not respond to any of the predictor variables, whilst epixylic species richness was negatively correlated with the percentage of large gaps, but this effect was only marginally significant (Table 7).

3.3. Drivers of bryophyte turnover

The significant variables for bryophyte species turnover, according to the Mantel test, were space, percentage of large gaps, management, stand surface area, thermicity index and elevation. Due to the high correlation between It and elevation (r = -0.85) two models, one with

Table 7. Summary results of GLMMs explaining terricolous (Terricolous bryophyte richness ~ elevation + (1| stand)), epiphytic (Epiphytic bryophyte richness ~ slope + (1| stand)) and epixylic bryophyte richness (Epixylic bryophyte richness ~ gaps + (1| stand)) with respect to plot predictors. Poisson error distribution for count data and log link function were used. Stand was included as a random factor. * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$.

Terricolous bryophyte richness ~ elevation + (1| stand)				
	Estimate	**Std. error**	**Z value**	**Pr (>|z|)**
(intercept)	0.5945	0.1063	5.595	2.20e-08***
Elevation	-0.5112	0.1028	-4.974	6.56e-07***

Epiphytic bryophyte richness ~ slope + (1| stand)				
	Estimate	**Std. error**	**Z value**	**Pr (>|z|)**
(intercept)	185.536	0.08416	22.047	<2e-16***
Slope	-0.1702	0.07188	-2.368	0.0179*

Epixylic bryophyte richness ~ gaps + (1| stand)				
	Estimate	**Std. error**	**Z value**	**Pr (>|z|)**
(intercept)	-0.713	0.2306	-3.092	0.00199**
Gaps	-0.5386	0.2912	-1.849	0.06438

elevation and a second one with It, were built. The final model obtained by MRM analysis explained 12.14% of species turnover with two variables, elevation and percentage of large gaps, with similar contributions, 6.65 and 5.34 respectively (Table 8).

Elevation was also the most important driver for the turnover of the analysed bryophyte groups: mosses, *moderately sensitive* and *long lived*. Particularly, elevation was the only driver for moss turnover. *Moderately sensitive* species turnover was driven by elevation and management, whose shared effect had a negative value. However, management intensity explained very little variation. *Long-lived* species turnover was explained by the same variables as bryophyte turnover; percentage of large gaps and elevation, and the model explained 13.46% with little shared effect (Table 8).

3.4. Indicator species analysis

The indicator species analysis (IndVal) for management categories showed that the only significant species ($p < 0.05$) was *Thuidium tamariscinum*, diagnostic for the category *low*. *Thuidium tamariscinum* had been classified as a *moderately sensitive* species regarding SMI. For the combination of the *low* and *moderate* categories three species were significant: *Schistidium crassipilum*, *Metzgeria furcata* and *Frullania tamarisci*. For the combination of the *moderate* and *high* category only *Ulota* sp. was significant, and it can correspond to one of three identified species, all classified as *moderately sensitive*. In view of the obtained results about elevation as driver of bryophyte turnover, we additionally performed the indicator species analysis regrouping the plots regarding the elevation (the plots below and over 1300 m). Diagnostic species for the lower elevations were *Atrichum undulatum*, *Ctenidium molluscum*, *Dicranum scoparium*, *Eurhynchium striatum*, *Frullania tamarisci*, *Hypnum cupressiforme* var. *cupressiforme*, *Isothecium myosuroides* subsp. *myosuroides*, *Metzgeria furcata*, *Neckera pumila*, *Plagiochila porelloides*, *Thuidium tamariscinum* and *Ulota* sp., whilst diagnostic species for the higher elevations were *Dicranum tauricum* and *Porella platyphylla*.

Table 8. Results of multiple regression on distance matrices analysis (MRMs) for bryophyte, moss, *moderately sensitive* bryophyte and *long-lived* bryophyte turnover in silver fir-beech stands from the western Pyrenees showing the unique and shared effects of significant variables. *Gaps*: percentage of large gaps.

Bryophyte turnover	**Variation explained (%)**
full model (*gaps* + elevation)	12.14
gaps effect	5.34
elevation effect	6.65
shared effect	0.15

Moss turnover	**Variation explained (%)**
full model (elevation)	6.07

***Moderately sensitive* bryophyte turnover**	**Variation explained (%)**
full model (management + elevation)	9.14
management effect	2.21
elevation effect	8.16
shared effect	-1.23

***Long-lived* bryophyte turnover**	**Variation explained (%)**
full model (*gaps* + elevation)	13.46
gaps effect	5.95
elevation effect	7.36
shared effect	0.15

4. DISCUSSION

4.1. General patterns

Our sampled plots contained almost all (90%) the indicator species reported by Delgado and Ederra (2010) for the suballiance *Scillo-Fagenion* (*Scillo-Fagetum* and *Carici-Fagetum* associations) in Navarre: *Atrichum undulatum*, *Brachythecium rutabulum*, *Ctenidium molluscum*, *Dicranium scoparium*, *Eurhynchium striatum*, *Exsertotheca crispa*, *Plagiochila porelloides*, *Polytrichum formosum*, *Rhytidiadelphus triquetrus* and *Thuidium tamariscinum*. Thus, our study confirms the indicator value of the mentioned species for the basophilous beech forests in this region.

A previous long-term study conducted in these western Pyrenean forests showed a decline in species richness and high turnover in 30 years, from 1982 to 2010 (Delgado and Ederra 2013). These authors suggested that these changes in the bryodiversity were linked to an increase in temperature and soil acidification on the broader scale and with changes in the canopy cover on the stand-scale. We have compared the bryophyte species list of the *Scillo-Fagetum* stands reported by Delgado and Ederra (2013) with the list we have compiled from five stands sampled in the same area. Total species richness was 22% lower in our list, which included only 50% of the species recorded by Delgado and Ederra (2013), although with 20 new species. Additionally, we confirm the presence of five species (*Ptychostomum capillare, Dicranella heteromalla, Homalothecium lutescens* var. *lutescens, Lophocolea heterophylla* and *Zygodon rupestris*) which were reported in 1982, and considered disappeared in 2010. These differences in species richness and composition were expected because of the different sampling methods applied. In particular, using the floristic habitat sampling conducted by Delgado and Ederra (2013) more species can be found than by the plot sampling conducted in our study (Newmaster et al., 2005).

According to our results, the proportion of long-lived bryophytes is high (over 60%) and similar among the management categories. Contrasting results were obtained in German beech forests in which the proportion of long-lived species was much lower in managed forests (Friedel et al., 2006). This high frequency of long-lived species in the western Pyrenean silver fir-beech forests, irrespective of their management intensity, may indicate that they are subject to small-scale disturbances, which is supported by the fact that the average value of *gaps* is low (5%). In fact, long-lived bryophytes are linked to stable environmental conditions as they have low reproductive effort and a long life span (During, 1979). Conversely, the short-lived bryophytes are more likely to be found just after disturbances as they have persistent spores, short life span and high sexual and asexual reproductive effort (Heinken and Zippel, 2004).

4.2. Bryophyte species richness

Bryophyte species richness was examined as overall bryophyte richness and as richness of species groups based on taxonomy, sensitivity to forest management, life cycle strategy and habitat preference. According to our results, overall bryophyte richness decreases with elevation (Table 3). Changes in bryophyte richness with elevation have already been reported by several studies which highlighted that the relationship between bryophyte richness and elevation may depend on the scale, thus a hump-shaped relationship is observed for the long elevational gradient, whilst for short gradients a linear pattern is characteristic (Grau et al., 2007; Spitale et al., 2009). In our case, bryophyte richness linearly decreased with elevation considering that the sampled gradient was relatively short. We interpret this effect as the overall climatic change along the elevational gradient. In the western Pyrenees the highest elevations correspond to the most continental part of the study area, hence the decrease in bryophyte richness with elevation might be due to higher continentality and higher temperatures during the summer months, which finally lead to fine scale differences in moisture conditions, known to affect bryophyte richness (Tng et al., 2009).

According to our results the effect of elevation was dependent on management category. The interaction between these two factors is expected; the stands on the higher elevations were less accessible for the wood extraction and the stands situated on the lower elevations were subjected to more intensive logging. Bryophyte richness was expected to be high in the stands in lower elevations, but in the interaction with intensive forest management these stands were species poor. Our results confirm that intensive forest management affects bryophyte richness. The low bryophyte richness in intensively managed stands can be explained by the deficiency of microhabitats (Halpern et al., 2014) and altered microclimatic conditions, which could inhibit higher species richness. In particular, in intensively managed Pyrenean forests management was oriented to logging the large fir trees (Sangüesa-Barreda et al., 2015), which can be considered as a loss of important microhabitats.

Surprisingly, forests with moderate and low management intensity did not differ in species richness, and this result can be interpreted twofold. On the one hand this could mean that moderately managed forests provide all necessary environmental conditions for bryophyte growth. On the other hand, in most of the unmanaged stands forest management is abandoned for only forty years, which might be too short period for the forest recovery in the sense of development of old-growth attributes and specific species diversity (Paillet et al, 2010). In addition, best preserved forests in the western Pyrenees are growing on high elevations, in which the tree growth is considerably affected by unfavourable climatic conditions (Burrascano et al., 2013); hence these almost unmanaged stands may show similar forest structure as managed ones in the terms of low basal area and biomass volume.

Similar results were reported in forests from the Czech Republic, in which managed forests with diverse tree structure and composition may host the same bryophyte richness as unmanaged ones (Hofmeister et al., 2015). Thus, it could be inferred that forest management is possible without reducing natural biodiversity, as long as management impact is not intensive. In an effort to compare our results with existing studies on this topic we assume that the general comparisons are context-sensitive. For instance, the criteria and categories used to describe managed and unmanaged forests across local studies differ since they comprise a high variety of management histories. In spite of this, our results regarding the decrease in bryophyte richness in intensively managed forests are consistent with the results of a meta-analysis comparing European managed and unmanaged forests, which reported lower bryophyte richness in the managed ones (Paillet et al., 2010).

Both liverwort and moss richness responded to elevation, but liverwort richness also decreased in the steeper slopes, which can be linked with harsher habitat conditions such as water and nutrient loss. Slope ranged from 10 to 76% in the sampled plots, hence in the steeper slopes the liverworts growing on dead wood, such as *Blepharostoma trichophyllum* var. *trichophyllum*, *Lepidozia reptans* and *Lophocolea heterophylla,* might be affected by the mobility and absence of dead wood substrate. Moreover, the number of epiphytessuch as *Frullania* sp., *Radula complanata* and *Metzgeria furcata* may decrease in the steeper slopes because these species might be exposed to higher light levels as well as drought, which have a great negative influence on liverworts (Sabovljević et al., 2010). We also detected a decrease of *sensitive* bryophyte richness with an increase in slope. In fact, 35% of the *sensitive* species found in these forest stands are liverworts, a high proportion taking into account that liverworts account only for 15% of the bryophytes found in this study. Additionally, the dead-wood specialist mosses *Buxbaumia viridis* and *Dicranodontium denudatum* are also included in this category.

Bryophyte classification according to sensitivity to forest management did not yield the expected results. In fact, *sensitive* species were present in all the management categories. In particular, *Buxbaumia viridis* was found only once in a stand assigned to the category of *moderate* intensity, which had been intensively managed in the past, probably by logging the largest fir trees, and later abandoned. In that particular stand, there was not any fir tree, but decomposed fir stumps remained as suitable habitat for *Buxbaumia viridis*. Furthermore, the *sensitive* species *Dicranodontium denudatum, Lescuraea incurvata*, *Scapania aspera* and *Serpoleskea confervoides,* were found only in stands which are under active management plans, assigned to the *moderate* category. Although *Antitrichia curtipendula*, *Isothecium alopecuroides*, *Ptegygnandrum filiforme* var. *filiforme* and *Radula complanta* were classified as sensitive species by Dierssen (2001), they were frequent in all the management categories in our study area. In fact, they are common species in the Pyrenean beech forests (Infante and Heras, 2008). Therefore, we advocate that these species cannot be considered indicators of forest management in the western Pyrenean forests and that the categories proposed by Dierssen (2001) about sensitivity to forest management are not applicable for the region covered by this study. The observed inconsistency between our results and the above-mentioned bryophyte classification might be explained by the fact that the observed management intensity gradient is not large enough to capturepossible differences in species richness. Studies conducted in boreal forests, using a different bryophyte classification (Trass et al., 1999), have shown that unmanaged forests are richer in sensitive species, but they also noticed that itis possible to find sensitive species even in intensively managed forests where they can resist in adequate microhabitats (Vellak and Ingerpuu, 2005).

The bryophytes groups regarding habitat preference did not show any relation with forest management and their richness was explained similarly to other groups by elevation and slope. This was especially surprising for epiphytic bryophytes which are known to be sensitive to forest management (Aude and Poulsen, 2000; Király and Ódor, 2010) as their diversity depends on the presence of large trees (Fritz et al., 2009). In this case epiphytic bryophytes were driven by slope rather that forest management intensity. As a consequence of nutrient loss and low soil productivity, in the steep slopes tree growth might be limited; hence the smaller trees found in such slopes might not provide sufficient bark area for epiphytic development as demonstrated by Fritz et al. (2009).

Long-lived bryophyte species richness expectedly decreased with elevation and management intensity, similarly to total bryophyte richness, as they contributed with 65 % to total bryophyte richness. Their richness also decreased with slope, which is a limiting factor for the persistence of these bryophytes as they need stable environmental conditions irrespective of their habitat preference. For instance, terricolous long-lived bryophytes might be affected by soil erosion, epiphytic long-lived species by limited bark area and epixylic long-lived by absence of deadwood. Conversely, short-lived species did not respond to any environmental factor because they are adapted to a high variability of microclimatic conditions (Heinken and Zippel, 2004), hence they can grow in forests subjected to different management intensities.

4.3. Bryophyte species turnover

According to the MRM results, the predictors of bryophyte turnover in the western Pyrenean forests were related to environmental heterogeneity, whilst space did not play any role. The environmental factors, elevation and percentage of large gaps, were operating independently. Elevation was one of the factors explaining bryophyte turnover just like for the bryophyte species richness model. As elevation is strongly correlated with climatic factors, such as ombrothermic and thermicity indices ($r = 0.68$ and $r = -0.86$, respectively), it can be assumed that the change in species composition is driven by a combination of these factors. Unlike species richness, bryophyte turnover was also driven by the percentage of large gaps (Table 8), which was also reported by Friedel et al. (2006), Tinya et al. (2009) and Raabe et al. (2010). This turnover caused by the percentage of large gaps suggests the presence of species adapted to higher light levels, described as photophytic (Dierssen, 2001). However, the photophytic species *Ceratodon purpureus* subsp. *purpureus, Homalothecium lutescens* var. *lutescens, Hygrohypnum luridum, Lescurea incurvata, Orthotrichum lyellii, Orthotrichum striatum, Palustriella commutata* and *Syntrichia ruralis* var. *ruralis* were recorded in plots with very low light levels (2.56% - 3.58%). Hence, this difference in species composition related to gap size could be due to the change of the microclimatic conditions, such as air humidity or temperature (Heilmann-Clausen et al., 2005; Király et al., 2013; Ódor et al., 2013).

The turnover of *moderately sensitive* species was mainly caused by elevation and secondarily by management intensity. As the shared effect between these two variables had a negative value we cannot separate clearly the effects of each variable. Indeed, negative values of shared effect may indicate correlation between variables, which is a common problem in variance partitioning techniques (Sabatini et al., 2014). Due to the little variance explained by management intensity and its correlation with elevation we cannot accurately determine the existence of management effect.

The results of the species indicator analysis showed that in the studied area *Thuidium tamariscinum* has preference for stands with low disturbance in the lower elevations. Rather than for management intensity, this species might be diagnostic for lower elevations under strong Atlantic influence in the western part of the studied area, according to the distribution area of this species (De Miguel and Ederra, 1984). Similarly, some of the diagnostic species for lower elevations such as *Frullania tamarisci*, *Isothecium myosuroides* subsp. *myosuroides, Neckera pumila* and *Ulota* sp. are more frequent in the western part of the studied area under major Atlantic influence (Lecointe, 1980; Heras, 1985). Conversely, the strong fidelity shown by *Dicranum tauricum* for the higher elevations in the eastern part of studied area might be explained by its affinity for high continentality.

5. CONCLUSIONS

Analyzing different aspects of bryophyte diversity in the western Pyrenean silver fir-beech forests our main result is that intensive forest management affects bryophyte species richness. Intensive forest management in this region comprises large tree logging and stand homogenization, which cause the loss of microhabitats and bryophyte diversity. Our results also showed that the moderately managed forests are well preserved, as in these stands the practice of sustainable forest management reconciles foresters and biodiversity conservation needs. We have also confirmed that richness is affected by elevation which, as a proxy of a combination of climatic factors, is one of the important drivers of species richness and species turnover. Our expectations were also to find more sensitive species in preserved forests which was not the case in the studied stands. Thus, we did not find bryophyte classification regarding bryophytes sensitivity to human impact as a suitable measure for evaluating forest management in any extent. Our recommendations for preserving bryophytes diversity are directed towards sustainable forest management. Instead of group selection logging or shelterwood, which are the methods historically used in the Pyrenean silver fir-beech forests, sustainable methods should be applied, such as low intensity selective logging, which somehow simulates natural forest dynamics. In such way species composition, forest structure diversity and quantity of dead wood is maintained. Besides, keeping forest continuity and diversity of microhabitats is crucial for bryophyte conservation, especially in the steep slopes which are prone to erosion.

ACKNOWLEDGEMENTS

We thank Daniel Garcia Magro for the help with field work, Marta Infante for helping in bryophytes identification and Hanna Tuomisto for valuable comments. Our sincerest thanks to our editor Robin Pakeman and to three anonymous reviewers, whose constructive comments helped us to improve this work.

Funds from the project IT299-10 for research groups of the Basque Government have been used for this survey.

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SUPPLEMENTARY MATERIAL

APPENDIX A. Characteristics of the sampled stands in the silver fir-beech forests from the western Pyrenees.

Stand	Elevation (m a.s.l.)	Stand's coordinates (x,y)	Stand surface area (ha)	Number of plots
Lizardoia	980-1080	0653820, 4763330	49	5
San Fermin	1000-1230	0655930, 4761810	49	5
Eskalera	990-1140	0654482, 4760315	30	4
Iturtxarra	990-1100	0651107, 4760302	35	4
Burdinzkoa	1140-1230	0653604, 4759107	30	4
Pikatua	1110-1300	0661514, 4758615	32	5
Maze	1320-1520	0677288, 4751014	68	5
Otsobieta	1300-1370	0676476, 4750586	32	5
Selva Grande	1250-1290	0676174, 4754505	81	4
Larondo	1263-1310	0671019, 4755772	73	1
Aztaparreta	1600-1650	0677940, 4753194	93	9
Gamueta	1340-1530	0679985, 4750580	82	5
Las Eras	1350-1420	0679594, 4749497	63	4
Selva de Oza	1200-1400	0686280, 4744519	32	5
Plana	1285-1340	0688166, 4744797	63	2
Pavo	1390-1410	0690065, 4746704	73	4

APPENDIX B. Bryopyhte species list in silver fir-beech forests in the western Pyrenees with indication of their taxonomic group, sensitivity to forest management, life strategy and substrate preference. S: sensitive bryophytes; M: moderately sensitive bryophytes; T: tolerant bryophytes; SL: short-lived bryophytes; LL: long-lived bryophytes.

Species	Taxonomy	Management sensitivity	Life-strategy	Substrate preference
Alleniella complanta	Moss	M	LL	Epiphytic
Anomodon viticulosus	Moss	M	LL	Epiphytic
Antitrichia curtipendula	Moss	S	LL	Epiphytic
Atrichum undulatum	Moss	T	SL	Terricolous
Blepharostoma trichophyllum var. *trichophyllum*	Liverwort	S	SL	Epixylic
Brachythecium rutabulum	Moss	T	LL	Opportunistic
Brachythecium velutinum var. *velutinum*	Moss	T	LL	Opportunistic
Bryoerythrophyllum recurvirostrum	Moss	M	SL	Opportunistic
Buxbaumia viridis	Moss	S	SL	Epixylic
Campylidium calcareum	Moss	M	LL	Epiphytic
Ceratodon purpureus subsp. *purpureus*	Moss	T	SL	Opportunistic
Cirriphyllum crassinervium	Moss	S	LL	Epilithic
Ctenidium molluscum	Moss	M	LL	Epilithic
Dicranella heteromalla	Moss	M	SL	Terricolous
Dicranodontium denudatum	Moss	S	LL	Epixylic
Dicranum scoparium	Moss	M	LL	Opportunistic
Dicranum tauricum	Moss	T	LL	Epiphytic
Encalypta streptocarpa	Moss	M	LL	Epilithic
Encalypta vulgaris	Moss	T	LL	Terricolous
Eurhynchiastrum pulchellum var. *pulchellum*	Moss	M	LL	Epilithic
Eurhynchium striatum	Moss	M	LL	Terricolous
Exsertotheca crispa	Moss	M	LL	Epiphytic
Fissidens dubius	Moss	M	LL	Opportunistic
Fissidens taxifolius subsp. *taxifolius*	Moss	T	SL	Terricolous
Fissidens viridulus var. *viridulus*	Moss	T	SL	Epilithic
Frullania dilatata	Liverwort	M	LL	Epiphytic
Frullania fragilifolia	Liverwort	S	LL	Epiphytic
Frullania tamarisci	Liverwort	T	LL	Epiphytic
Grimmia hartmanii	Moss	M	LL	Epilithic
Grimmia sp.	Moss	-	-	-
Herzogiella seligeri	Moss	M	LL	Epixylic
Homalothecium lutescens var. *lutescens*	Moss	M	LL	Terricolous
Homalothecium philippeanum	Moss	M	LL	Epilithic
Homalothecium sericeum	Moss	M	LL	Epiphytic
Hygrohypnum luridum	Moss	M	LL	Epilithic
Hylocomium splendens	Moss	M	LL	Terricolous
Hypnum cupressiforme var. *cupressiforme*	Moss	T	LL	Opportunistic
Isothecium alopecuroides	Moss	S	LL	Epiphytic
Isothecium myosuroides subsp. *myosuroides*	Moss	M	LL	Epiphytic
Kindbergia praelonga var. *praelonga*	Moss	T	LL	Epilithic
Kindbergia praelonga var. *stokesii*	Moss	T	LL	Epilithic
Lepidozia reptans	Liverwort	M	SL	Opportunistic
Lescuraea incurvata	Moss	S	LL	Epilithic
Lophocolea bidentata	Liverwort	T	LL	Terricolous

APPENDIX B (Cont.).

Species	Taxonomy	Management sensitivity	Life-strategy	Substrate preference
Lophocolea heterophylla	Liverwort	S	SL	Epixylic
Metzgeria furcata	Liverwort	M	LL	Epiphytic
Mnium hornum	Moss	M	LL	Terricolous
Neckera pumila	Moss	M	LL	Epiphytic
Orthotrichum affine	Moss	T	SL	Epiphytic
Orthotrichum cupulatum var. *cupulatum*	Moss	T	SL	Epilithic
Orthotrichum lyellii	Moss	T	LL	Epiphytic
Orthotrichum rupestre	Moss	T	SL	Epilithic
Orthotrichum shawii	Moss	M	SL	Epiphytic
Orthotrichum stramineum	Moss	T	SL	Epiphytic
Orthotrichum striatum	Moss	M	SL	Epiphytic
Oxyrrhynchium speciosum	Moss	M	LL	Opportunistic
Palustriella commutate	Moss	T	LL	Epilithic
Pellia endiviifolia	Liverwort	T	SL	Epilithic
Plagiochila porelloides	Liverwort	M	LL	Opportunistic
Plagiomnium undulatum var. *undulatum*	Moss	T	LL	Terricolous
Plagiothecium curvifolium	Moss	M	LL	Opportunistic
Plagiothecium nemorale	Moss	M	LL	Opportunistic
Plasteurhynchium striatulum	Moss	S	LL	Opportunistic
Pogonatum aloides	Moss	T	SL	Terricolous
Polytrichum formosum	Moss	M	LL	Terricolous
Porella platyphylla	Liverwort	M	LL	Epiphytic
Pseufotaxiphyllum elegans	Moss	M	SL	Terricolous
Pterigynandrum filiforme var. *filiforme*	Moss	S	LL	Epiphytic
Ptychostomum capillare	Moss	T	SL	Opportunistic
Radula complanata	Liverwort	S	LL	Epiphytic
Rhizomnium punctatum	Moss	M	LL	Epixylic
Rhytidiadelphus triquetrus	Moss	M	LL	Terricolous
Scapania aspera	Liverwort	S	SL	Epilithic
Schistidium crassipilum	Moss	T	SL	Epilithic
Schistidium sp.	Moss	-	-	-
Serpoleskea confervoides	Moss	S	LL	Epilithic
Syntrichia ruralis var. *ruralis*	Moss	M	SL	Epilithic
Tetraphis pellucid	Moss	M	SL	Epixylic
Thamnobryum alopecurum	Moss	M	LL	Epilithic
Thuidium tamariscinum	Moss	M	LL	Terricolous
Tortella tortuosa var. *tortuosa*	Moss	M	LL	Opportunistic
Tortula marginata	Moss	T	SL	Epilithic
Tortula subulata	Moss	T	SL	Epilithic
Trichostomum brachydontium	Moss	M	LL	Terricolous
Ulota bruchii	Moss	M	SL	Epiphytic
Ulota crispa	Moss	M	SL	Epiphytic
Ulota crispula	Moss	M	SL	Epiphytic
Zygodon rupestris	Moss	T	SL	Epiphytic

chapter 4

Vlatka Horvat (2018) PhD THESIS pp. 85-98

Managed and unmanaged silver fir-European beech forests show similar structural features in the western Pyrenees

ABSTRACT Forest structure is considered one of the basic features of the forest ecosystem and widely studied with the aim to develop sustainable management strategies. The approach for this purpose is usually based on the comparison of stand structural features in the managed and unmanaged forests. Managed stands are somehow disturbed by silvicultural practices, whilst unmanaged ones are subject to natural disturbance dynamics and may serve as a reference for studies on forest management. Pyrenean silver fir-beech forests are understudied regarding this topic, and the evaluation of the structure of managed and unmanaged stands is still missing. In this work, we compared currently managed stands and those unmanaged for at least 40 years. Man Whitney´s U test was used to test for differences between managed and unmanaged stands, regarding the selected stand parameters. Stand structure did not differ significantly between management categories. Pyrenean silver fir-beech stands showed a tendency towards a J-shaped diameter distribution, regardless of their management type. Our results indicate that the managed stands preserved the recommended diameter distribution although they have been intensively managed in the past, whilst unmanaged ones are still on the way to develop old-growth attributes because management abandonment is recent for significant changes in forest structure.

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KEY WORDS ***Abies alba*; *Fagus sylvatica*; Forest management; Gaps; Pyrenees; Stand structure**

PUBLISHED **Under review in *iForest***

ABBREVIATIONS DBH, diameter-at-breast-height.

1. INTRODUCTION

Stand structure as a functional feature of forest ecosystem (Pretzsch, 1997) is the result of the relationships among the individuals and the environment through competitive processes and biomass control (Townsend et al., 2003). The general description of forest structure refers to a horizontal and vertical spatial distribution of plant species (Zenner and Hibbs, 2000). Determined by tree species composition, stand dynamics, stand conditions and natural disturbances, forest stand structure is also directly affected by forest management. Silvicultural practices considerably change horizontal and vertical stand structure creating gaps in the forest canopy and changing the light regime. Subsequently, gap creation initiates the regeneration processes in the understory, affecting the stand dynamics (Yamamoto, 2000). Microclimate in the understory is also dependent on canopy structure, particularly canopy density (Arx et al., 2012). Moreover, forest structure may influence edaphic conditions such as soil water content, pH, temperature and nutrient availability (Barbier et al., 2008). As forest structure strongly influences environmental conditions in the understory, it has been considered a key factor determining biodiversity patterns in forest ecosystems (Gao et al., 2014). The assessment of management effect on stand structure requires the estimation of stand parameters such as diameter distribution, tree density, tree heights, canopy closure and dead wood quantity. Given the importance of the forest structure, modern forestry strives to harmonise the economical and ecological needs, implementing adequate management methods. The idea of sustainable forest management is based on emulating natural processes, which can be studied in unmanaged forests. Because of their natural dynamics, unmanaged forests provide valuable information for developing management strategies and effective conservation policies (Burrascano et al., 2013). In contrast, the natural processes are somehow disturbed in managed forests and disturbance intensity depends on the management type applied.

Up to now, forest structure evaluation for managed and unmanaged forests has been assessed in many European forests (Boncina, 2000; Bianchi et al., 2011; Bilek et al., 2011; Sitzia et al., 2012; Schütz et al., 2016), whilst this issue remains scarcely studied in the Pyrenean forests (but see Gil Pelegrín et al., 1989). Silver fir (*Abies alba* Mill.)-beech (*Fagus sylvatica* L.) forests in the Pyrenees have been managed over the centuries, but their management history is not completely clear as the silvicultural practices in the Pyrenean forests were scarcely documented. According to the available information about management history in this region (Navarra, 2000), most of the western Pyrenean forests were overexploited in the beginning of the 20th century, either by timber exploitation or grazing. Management types in these mixed stands were frequently changed, from selection system, shelterwood, clearcuts or exclusively silver fir logging. In the last 50 years, human migrations and the abandonment of these activities led to an increment of forest cover and growing stock (Navarra, 2000). Currently, in the western Pyrenees most of the forests are subjected to regular management plan, which promotes sustainable forest management (Navarra, 2000), except the areas included in the natural parks or strict reserves, which remain unmanaged.

In the context of forest management in the Pyrenees, the present study aims to provide for the first time a detailed characterisation of the structural attributes of these mixed mountain forests and to compare managed and unmanaged stands regarding selected stand parameters. We hypothesised that stand structure would differ between actively managed stands, intensively managed in the past, and well-preserved remnants never subjected to intensive forest management and withdrawn from the management plans 40 years ago.

2. MATERIAL AND METHODS

2.1. Study area

The study area is located in the western part of the Pyrenean mountains, specifically in the Spanish part of massive, encompassing the regions of Navarre and Aragón (Fig. 1). The landscape is characterised by valleys and mountains stretching in west-east direction in the elevation range from 1,800-2,500 m above the sea level. Bedrock is formed by limestone and marly flysch with brown soils. Biogeographically, this area belongs to the Alpine Region and according to the Global Bioclimatic Classification System developed by Rivas-Martínez (2007), the bioclimate is temperate oceanic, with a mean annual temperature of 8°C, mean annual rainfall of 1,419 mm and a W-E continentality gradient. A long history of livestock and forest exploitation has shaped the landscape in this area, which is highly heterogeneous and, in the beech belt contains semi-natural grasslands, scrublands, natural forests and *Pinus sylvestris* L. plantations. In the western Pyrenean beech belt, silver fir reaches its southwestern distribution limit, growing in mixed stands together with beech and even dominates some stands. The silver fir-beech forests of the study area are included in the association *Scillo lilio-hyacinthi-Fagetum sylvaticae* Br.-Bl. ex O. Bolòs 1957, which encompasses omprophilous hyperhumid forests (Rivas-Martínez et al., 1991). The management history of these stands is unclear because of unsystematically conducted silvicultural practices with different intensities during the last century. According to Navarra (2000) a high variety of management types were documented (single and group selection system, shelterwood, and exclusive fir exploitation). Within the studied area, the westernmost stands were recently managed, subjected to a management plan and historically have been intensively managed, whilst the easternmost stands have mostly been abandoned for at least 40 years, have never have been intensively managed and belong to natural parks and strict reserves.

2.2. Sampling design

We identified all north-facing stands of silver fir-beech forests in an altitudinal range between 800 and 1,700 m a.s.l, exceeding 30 ha. Twenty stands fulfilled these criteria encompassing approximately 700 ha, out of which we selected the unmanaged ones first. The rarity of well-

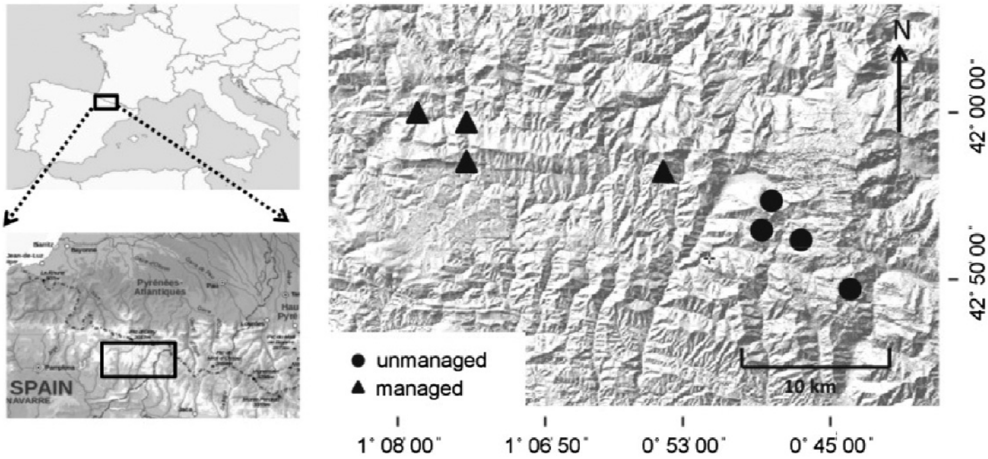

Fig. 1. Study area and location of the eight sampled stands in the western Pyrenees, provinces of Navarre and Aragón, N Spain.

preserved forests in the western Pyrenees did not allow us to sample more than four unmanaged stands. In order to have a balanced sampling design, four managed stands with similar site conditions and general stand characteristics, according to current management plan (Navarra 2000), were selected. As managed, we considered recently managed stands (managed from 5 to 20 years ago), whilst as unmanaged, we considered the stands withdrawn from the regular management in which timber harvesting has not occurred for more than 40 years. Within each management category, four stands were chosen, and within each stand, four plots were randomly sampled. This resulted in a total of 32 plots in eight clusters (Fig. 1). Field sampling was carried out in 2015 with permits from the Government of Navarre and Aragón.

Stand structure sampling was based on measuring diameter-at-breast-height (DBH) for all trees within three concentric circles with radii of 4, 13 and 20 m. In each concentric circle, we recorded all standing trees (living and dead) exceeding a pre-established diameter (DBH) threshold, which was 2.5 cm for the 4-m radius circle, 10 cm for the 13-m radius circle and 50 cm for the 20-m radius circle. For the dead standing trees, we used the term "snags". For deadwood quantification, the diameter of all the lying dead wood components (logs) with a minimum diameter ≥ 10 cm was recorded within the 13-m radius circle. For dead wood components, their decay stage was recorded according to Hunter (1990), distinguishing five decay classes from freshly fallen (decay class 1) to heavily decomposed (decay class 5). The tree heights were measured with the Haglof Vertex hypsometer for five individuals out of those whose DBH was measured, in total 160 trees randomly chosen within the sampled stands. The living wood volume was not calculated due to the lack of volume tables for this area.

Similar to Paillet et al. (2015), we distinguished four diameter categories for living trees: very large trees (DBH ≥ 67.5 cm), large trees (47.5 ≤ DBH < 67.5 cm), medium trees (22.5 ≤ DBH < 47.5 cm) and small trees (7.5 ≤ DBH < 22.5 cm).

To express structural diversity, the coefficient of variation of the diameter distribution (*VarD*), according to Sterba and Zingg (2006), was calculated for each plot. Here, *VarD* is a distance-independent indicator of the vertical structure of a forest stand, calculated as follows: $VarD = 100 \times sdDBH/xDBH$, where sdDBH is the standard deviation of the DBH classes and xDBH is the mean DBH.

To evaluate the stand structure we used the LikeJ index (Hanewinkel et al., 2014), which describes forest structure closeness to the J shape. This index is based on the number of stems per hectare in different diameter classes; the maximum value of closeness to the inverse J shape is 10 (Hanewinkel et al., 2014). Traditionally, the desirable diameter distribution of managed uneven-aged forests has been described by the inverse J-shaped distribution (O'Hara and Gersonde, 2004). However, diameter distribution of many old-growth forests, which could serve as a model, showed variety of diameter distribution shapes (Westphal et al., 2006).

Variables of light conditions (Table 1) were obtained by hemispherical photography. A detailed protocol of light sampling and analysis is described in Horvat et al. (2017). We calculated the following variables: transmission, which is a measure of overall canopy openness or total gap fraction; and gaps, the proportion of large between-crown gaps.

2.3. Data analysis

Stand structural features of managed and unmanaged stands are represented in figures and tables compiled for easier data visualisation. Differences between the management categories regarding selected stand parameters and topographic variables were assessed by Mann-Whitney´s U test (Table 1). To compare the tree heights between managed and unmanaged stands,

Table 1. Topographic and stand structural variables for 32 plots used in the comparison of managed and unmanaged stands in the western Pyrenean silver fir-beech forests. Differences between managed and unmanaged stands were tested using Mann-Whitney´s U test. * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$.

Variables	Unit	Managed Mean±SD	Unmanaged Mean±SD	*p* value
Topography				
Elevation	m a.s.l.	1118±104.70	1447±140.76	5.096e-06***
Slope	%	46.62±16.21	39.19±12.40	0.19
Light conditions				
Transmission	%	10.81±6.13	11.20±2.67	0.36
Gaps	%	6.7±5.50	5.9±2.28	0.89
Forest structure				
Tree density	(N/ha)	638±286	806±617	0.83
Beech density	(N/ha)	517±389	783±650	0.25
Fir density	(N/ha)	188±130	111±16	0.03*
Density of small trees	(N/ha)	11.25±8.31	13.56±10.22	0.52
Density of medium trees	(N/ha)	10.43±5.42	7.18±4.57	0.07
Density of large trees	(N/ha)	5.00±2.50	4.43±2.03	0.30
Density of very large trees	(N/ha)	0.75±0.93	1.93±1.94	0.09
Density of very large fir trees	(N/ha)	3.97±5.81	12.43±15.90	0.20
Density of very large beech trees	(N/ha)	1.98±6.16	2.98±5.71	0.42
Basal area of living trees	(m^2/ha)	34.95±9.41	35.20±12.61	0.79
Basal area of beech	(m^2/ha)	21.66±7.89	22.93±9.31	0.53
Basal area of fir	(m^2/ha)	14.37±11.06	14.51±17.13	0.44
Basal area of snags	(m^2/ha)	1.21±2.47	2.27±2.70	0.08
Basal area of logs	(m^2/ha)	3.89±3.91	2.21±1.80	0.46
Basal area of total dead wood	(m^2/ha)	5.09±4.18	4.53±2.77	0.95
Number of stumps	(N/plot)	3.68±2.86	2.18±3.63	0.05
VarD		50.40±18.23	62.36±17.77	0.06
LikeJ index		6.05±2.05	4.95±1.68	0.10

non-linear regression was performed, which permits tree height prediction on observed DBH. The regression was fitted using the power equation $H = a(DBH)^b$ (Huang et al., 1992), in which *D* is the DBH of each tree, *H* is the tree height and *a* and *b* are parameters to estimate.

3. RESULTS

The tree layer was dominated by beech (*Fagus sylvatica*), followed by silver fir (*Abies alba*), whilst the tree species *Acer opalus* Mill., *Sorbus aucuparia* L., *Salix caprea* L. and *Tilia platyphyllos* Scop. have been recorded as saplings (Horvat et al., 2017). The largest tree found was a silver fir of 140 cm DBH and 28.8 m high, growing in the best-preserved forest Aztaparreta, located below the timberline at an elevation of 1,600 m.

"Transmission" and "gaps" were highly correlated variables. Transmission average was 11.1%, thus the percentage of large gaps describes more than half of the canopy openness (mean percentage of large gaps was 6.34%). The percentage of large gaps did not differ significantly between managed and unmanaged stands (Table 1).

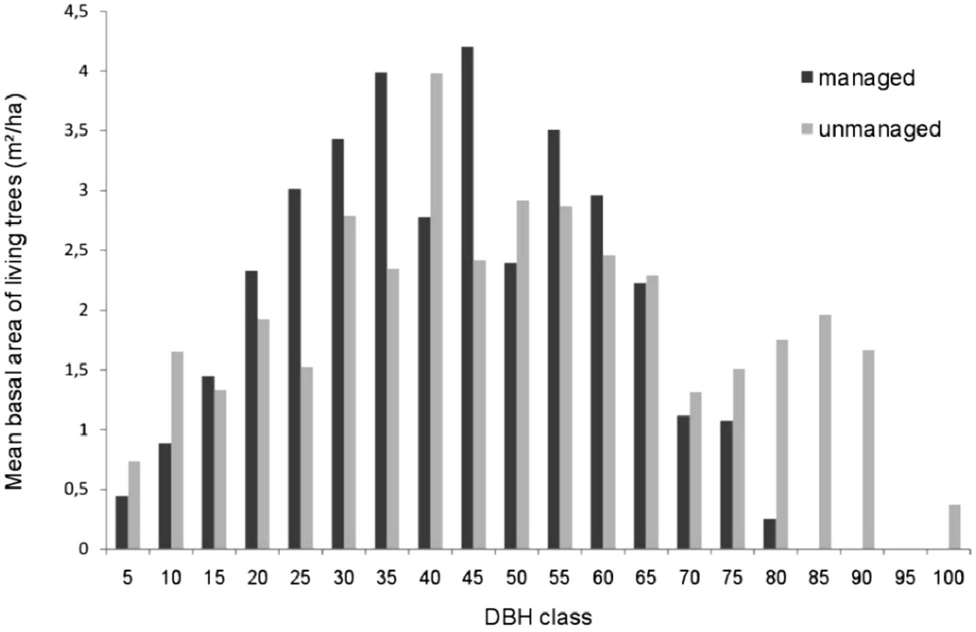

Fig. 2. Distribution of basal area of living trees by DBH classes in managed and unmanaged stands of silver fir-beech forests in the western Pyrenees.

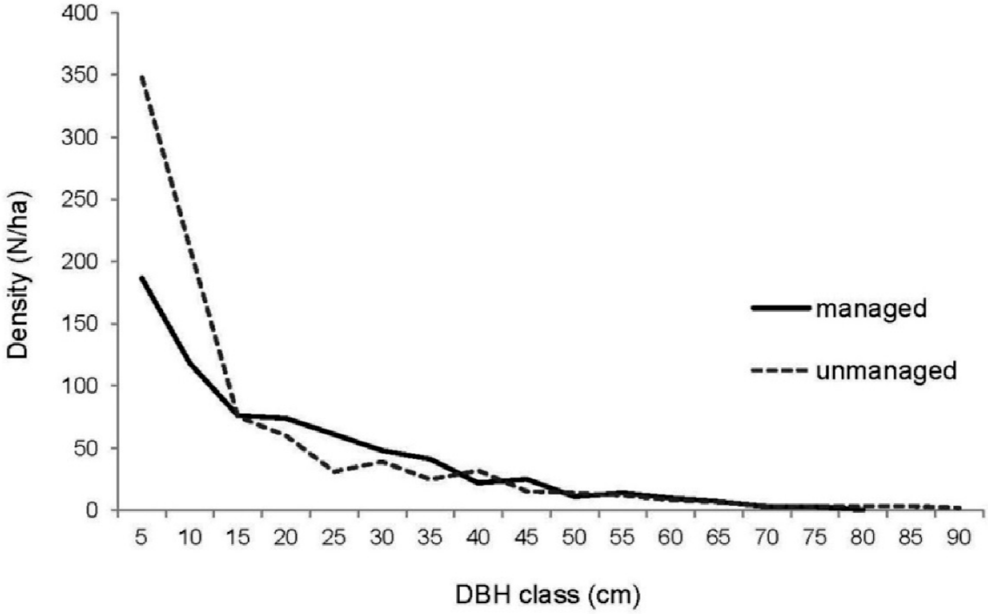

Fig. 3. Diameter distribution in the managed and unmanaged stands of silver fir-beech stands in the western Pyrenees.

Table 2. Percentage of dead wood across the decay classes in managed and unmanaged stands in silver fir-beech forests in the western Pyrenees.

	% of total dead wood per plot	
Decay class	**Managed**	**Unmanaged**
1	24.10	33.33
2	34.94	43.94
3	22.89	19.70
4	15.66	3.03
5	2.41	0

The basal area of living trees per hectare did not differ significantly ($p > 0.05$) between managed and unmanaged stands (Table 1). The differences regarding the basal area of small, medium, large and very large trees were not significant either (results not shown). However, trees in diameter classes over 85 cm were absent in the managed stands (Fig. 2).

Similar to mean basal area**,** tree density did not differ significantly between managed and unmanaged stands ($p > 0.05$; Table 1, Fig. 3). The density of small, medium, large and very large trees did not differ either (Table 1). When tree species were analysed separately, there was no significant difference in beech density between managed and unmanaged stands ($p > 0.05$), but the density of silver fir was significantly greater in the managed ($p < 0.05$; Table 1).

The LikeJ index in the sampled stands varied from 1.6 to 10, with no significant differences between managed and unmanaged stands ($p > 0.05$), although unmanaged stands tended to have lower LikeJ values (Fig. 4).

The basal area of dead wood did not differ between managed and unmanaged stands (Table 1). Decay class 2 was the most represented class in all the stands, and decay class 5 was absent in unmanaged stands (Table 2).

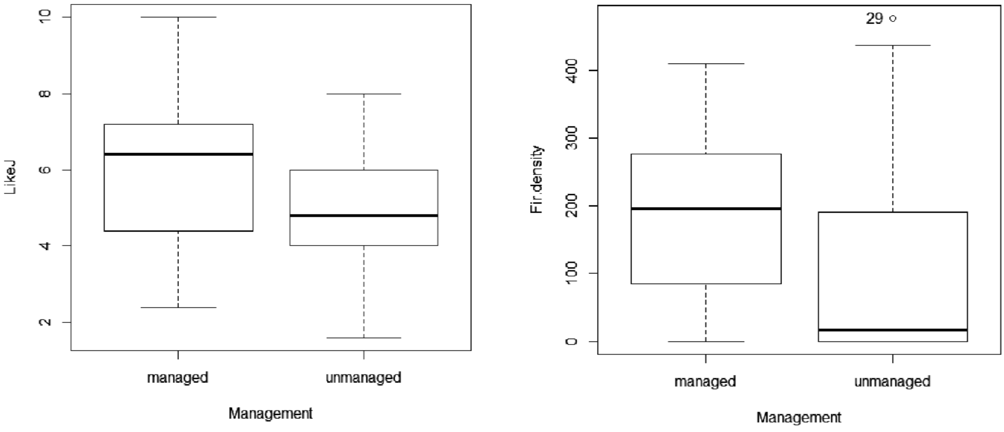

Fig. 4. (Right) Boxplot of fir density per hectare in managed and unmanaged stands of silver fir-beech forests in the western Pyrenees. Fir density was significantly higher in managed stands than in unmanaged ones ($p < 0.05$). (Left) Boxplot of LikeJ index, closeness to an inverse J shape, in the managed and unmanaged silver fir-beech stands from the western Pyrenees. Regarding the LikeJ index, managed and unmanaged stands did not differ significantly ($p > 0.05$). Maximum value of LikeJ index is 10, describing desirable stand structure for uneven-aged managed forests.

The height-diameter model for beech in managed and unmanaged stands showed a low fit ($R^2 = 0.33$ and $R^2 = 0.41$) because of the high height variability in the same DBH class. However, differences in height were unnoticeable between management types. The silver fir height model had a better fit in both managed and unmanaged stands ($R^2 = 0.71$, $R^2 = 0.83$), and slightly different curves were obtained for managed and unmanaged forests. In managed stands, silver fir of DBH = 60 cm reached a greater height than in unmanaged stands (Fig. 5).

4. DISCUSSION

Canopy openness in the studied Pyrenean forests showed low mean values both in managed and unmanaged stands (approximately 10 %), suggesting a rather closed canopy. The values of gap fraction measured in the sampled forests are in the range of the values reported for unmanaged stands in Central Europe, in which gap fraction varies between 3 and 16 % (Kucbel et al., 2010). The low gap fraction and the small size of gaps suggest that unmanaged Pyrenean forests follow the small-scale disturbance pattern without large disturbances. This pattern is also found in other well-preserved beech forests (Rugani et al., 2013, Hobi et al., 2015). In the case of managed Pyrenean stands, low gap fraction and small gap size (never exceeding 400 m^2) might suggest that the management type applied is not intense and emulates the natural forest dynamics. However, the results of the actual gap fraction only provide a static forest image (Kenderes et al., 2008), and further research on gap dynamics is needed to make sounder conclusions.

Comparing Pyrenean unmanaged stands with European old-growth forests (Burrascano et al., 2013), our stands showed a lower mean basal area per hectare. Pyrenean unmanaged stands were located on the highest elevations, in which low soil productivity and unfavourable climatic conditions can potentially affect tree growth and basal area (Burrascano et al., 2013). However, we attribute this lower basal area to a short period of forest abandonment. To support our conclusion that forest management has a negative effect on basal area, more likely than the elevation, we give the evidence of the presence of large fir trees in the old-growth

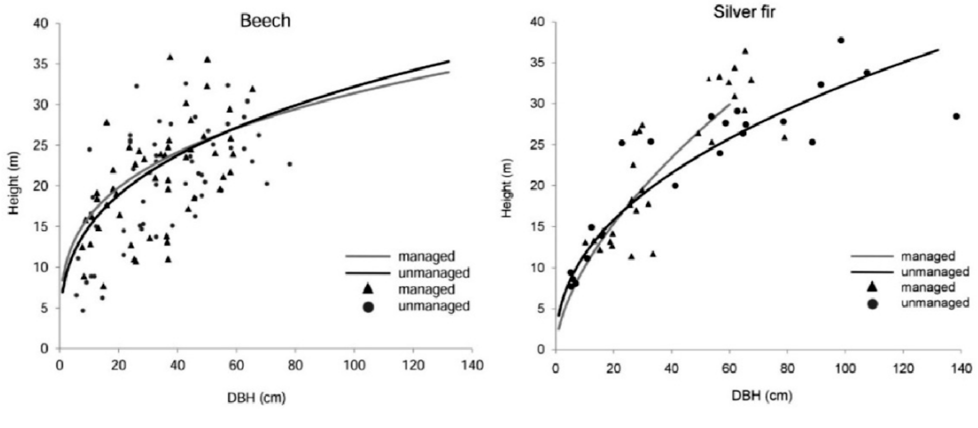

Fig. 5. Height-diameter models of beech and silver fir for managed and unmanaged stands in the western Pyrenees. The equation for the beech trees in the managed stands is $h = 8.3 \times DBH^{0.287}$, with $R^2 = 0.33$; for unmanaged stands, $h = 6.973 \times DBH^{0.332}$, with $R^2 = 0.41$. The equation for the fir trees in the managed stands is $h = 2.5 \times DBH^{0.666}$ with $R^2 = 0.71$; for unmanaged stands, $h = 4.17 \times DBH^{0.444}$, with $R^2 = 0.83$.

forest Aztaparreta, situated in the highest elevations. Similar spatial pattern of managed and unmanaged forests situation regarding elevational gradient have also been reported for the beech forests in the Apennines (Piovesan et al., 2005).

Although we did not find differences between unmanaged and managed stands regarding basal area, we observed a shift in the distribution of basal area towards larger diameter classes (> 80 cm) in unmanaged stands, which could be a consequence of management abandonment. This leads us to infer that these stands are in the ongoing process to reach the terminal phase. Similar conclusions were drawn for French forest reserves, in which the mean time of management abandonment was 46 years (Paillet et al., 2015).

Regarding diameter distribution, both managed and unmanaged stands showed the tendency to a J-shaped distribution (Fig. 3), which was a commonly adopted curve form described for uneven-aged forests in the equilibrium state (Rubin et al., 2006), although unmanaged stands can perform a variety of diameter distribution forms, such as a rotated sigmoid or a bimodal form and be considered in the equilibrium state as well (Schwartz et al., 2005; Westphal et al., 2006). Although tree density was similar among managed and unmanaged stands for the categories of small, medium, large and very large trees, the tree densities slightly changed among management types, showing different tendencies (Fig. 3). The main observed difference was that unmanaged stands tend to have a higher density of very small trees, and therefore, their diameter distribution is more distant from the J shape than that of managed stands. In fact, the minimum value of the LikeJ index was measured in the best-preserved forest Aztaparreta, subject to natural dynamics, in which biomass is accumulated in the largest DBH classes. Medium LikeJ values in the managed Pyrenean forests may reflect the mixture of management types used in these forests. Assuming that forest sustainability can be evaluated by diameter distribution (Rubin et al., 2006), Pyrenean forests can be considered as relatively stable systems (Schütz, 2001; Paluch, 2005), with unmanaged forests being in the recovery stage.

Regarding tree species proportion, the greater silver fir density in the managed stands may be a consequence of recent forest management favouring silver fir. Since silver fir decline has been confirmed in this area (Oliva and Colinas, 2007), forest managers adapt the management in order to preserve this tree species (Navarra 2000). Lower fir density in the unmanaged stands could mean that silver fir does not regenerate well, for instance due to beech dominance (Dobrowolska, 1998). However, the lack of fir regeneration still remains an open question (Oliva and Colinas, 2007).

The height-diameter model for beech showed high height dispersion across the diameter classes, which means that the beech trees with similar diameter had very different heights. This observation could be explained by the fact that beech is a shade-tolerant species, with saplings of up to 35 years (Collet et al., 2008). In these multilayered stands with low light availability, height growth is low, but when the canopy opens, saplings take advantage and grow quickly in height (Nagel and Diaci, 2006; Rugani et al., 2013). The same findings have been reported for beech forests in which the upper storey beech trees of 22 m had a wide range of diameters, from 20 to 100 cm (Commarmot et al., 2005; Rugani et al., 2013).

As regards to fir height-diameter model, the firs of the DBH class 60 cm were higher in the managed stands than in the unmanaged ones probably as combination of temperature effect and past forest management, which removed beech competition for light, water and nutrients to favour fir growth. This interpretation is consistent with our previous finding of a higher fir density in the managed stands. Tree heights may also depend on site quality; in particular silver fir stand productivity depends on rainfall and temperature, rather than on soil properties

(Becker, 1989; Pinto et al., 2008). In the sampled stands soil properties are similar regarding clay percentage, organic matter and nitrogen (Horvat et al., unpublished results), hence we exclude the potential effect of these factors. Annual precipitation does not differ between managed and unmanaged stands, although they are spatially clustered in our study, hence the water availability should not be a limiting factor.

Another observed feature in managed forests is the absence of large fir trees, which is also a consequence of past forest management, oriented towards the logging of large silver firs (Sangüesa-Barreda et al., 2015).

Surprisingly, the basal area of total dead wood did not vary between managed and unmanaged stands, contrasting the findings of many other studies (Motta et al., 2013; Silver et al., 2013). This indicates that forest managers are applying appropriate management strategies, mainly in terms of retaining a certain quantity of logs and snags to facilitate biodiversity. Although fewer stumps were counted in unmanaged stands, the number of stumps did not differ significantly between management categories, which confirms their recent abandonment, taking into account that total decomposition of beech coarse woody debris occurs over a period of about 35 years (Müller-Using and Bartsch, 2009). However, more detailed studies on dead wood quantity are needed, as in this study, we only refer to the dead wood basal area as an approximation for dead wood quantity.

5. CONCLUSIONS

Although the managed and unmanaged Pyrenean forests show a similar forest structure, unmanaged forests show a tendency to have less stumps, a higher density of small trees and an increased basal area in larger DBH classes. These observed trends suggest that the unmanaged silver fir-beech forests are still recovering and have not reached the terminal phase. Since management ceased approximately 40 years ago, these forests have not yet developed clear old-growth attributes, as the recovery of ecosystems after management cessation is a rather slow process. Our study may serve as a base for establishing the monitoring of unmanaged stands in the western Pyrenees.

Managed forests showed a high diameter variation, indicating a sustainable forest management, although they were intensively managed in the past. The guidelines for the future forest management should consider the maintenance of the current structural diversity, and increase the number of large trees as biodiversity hotspots. Future forest management should focus on the preservation of the natural proportion of fir and beech, even though the silver fir decline might justify that the forest management is directed towards a preference of this species.

ACKNOWLEDGEMENTS

We thank Almudena Pereda and Raul Ilundain for help with field work and Francesco Sabatini and Sabina Burrascano for assistance with the sampling protocol. Funds from the project IT299-10 for research groups of the Basque Government were used for this study.

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SUPPLEMENTARY MATERIAL A

Characteristics of the sampled stands in the silver fir-beech forests from the western Pyrenees.

Stand	Management category	Elevation (m a.s.l.)	Stand's coordinates (x,y)	Stand surface area (ha)
Lizardoia	managed	980-1080	0653820, 4763330	49
San Fermin	managed	1000-1230	0655930, 4761810	49
Eskalera	managed	990-1140	0654482, 4760315	30
Pikatua	managed	1110-1300	0661514, 4758615	32
Maze	unmanaged	1320-1520	0677288, 4751014	68
Aztaparreta	unmanaged	1600-1650	0677940, 4753194	93
Gamueta	unmanaged	1340-1530	0679985, 4750580	82
Selva de Oza	unmanaged	1200-1400	0686280, 4744519	32

chapter 5

Vlatka Horvat (2018) PhD THESIS pp. 99-123

Similar plant species diversity in managed and unmanaged silver fir–beech forests in the western Pyrenees

ABSTRACT

We studied the potential impact of forest management on plant diversity in silver fir–beech forests in the western Pyrenees. Earlier studies on this topic have mostly focused on vascular plants, although bryophytes are considered more sensitive for forest management impact. We surveyed plant species composition, stand structure, light conditions and soil properties in 32 plots representing both managed and unmanaged stands. For a more detailed insight, we divided the plant species into ecological groups. These were based on habitat preference for vascular plants and life strategy for bryophytes. We assessed potential drivers of species richness and species turnover by general linear mixed models and multiple regressions on distance matrices, respectively. Although managed and unmanaged stands turned out to be structurally similar, alpha richness of both vascular plants and bryophytes was higher in managed than in unmanaged forests. Both kinds of forest contained a high percentage of long-lived bryophytes, and had similar numbers of sensitive bryophytes. The main factors explaining species richness were elevation, percentage of large gaps and soil silt content for vascular plants, and elevation and soil aluminium saturation for bryophytes. Forest management was not related to species richness in either plant group. Species turnover of vascular plants was best explained by geographical distance and differences in percentage of large gaps, number of large fir trees and soil aluminium saturation. The only variable that significantly explained bryophyte species turnover was geographical distance. We found that the assemblages of vascular plants and bryophytes can respond differently to environmental variables in the study area, so studying them separately can give a more nuanced view on community heterogeneity than treating all plants together.

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KEY WORDS **Bryophytes; Forest management; Stand structure; Gaps; Soil properties; Vascular plants**

PUBLISHED **Under preparation for submission**

ABBREVIATIONS AIC, Akaike Information Criterion; GLMM, Generalized Linear Mixed Model; LAI, Leaf Area Index; LCS, life cycle strategy; MRM, Multiple regression on distance matrices; SMI, bryophyte sensitivity to forest management.

1. INTRODUCTION

Species diversity is considered important for ecosystem functioning (Tilman et al., 1997), so there is an increasing need to understand diversity patterns and their determinants in order to promote sustainable forest management (Parviainen, 2005) and effective conservation policy (Burrascano et al., 2013). Management can substantially change forest structural features, which has both direct and indirect consequences for light conditions (Tinya et al., 2009), edaphic conditions (Barbier et al., 2008) and species diversity (Sebastià et al., 2005; Burrascano et al., 2009). Unmanaged forests may host rare species and contain higher species diversity than managed forests, because natural dynamics tends to provide more structural variation and higher diversity of microhabitats than standard forest management does (Økland et al., 2004). Old-growth structural features (such as large living trees, senescent trees and dead wood) are absent in managed forests (Commarmot et al., 2005), which can threaten plant species dependent on such habitats (Bengtsson et al., 2000).

However, the overall assessment of forest management effects on biodiversity has given variable results. In many local studies, unmanaged stands had no higher richness of vascular plants and bryophytes than managed sites did (Schmidt, 2005; Müller et al., 2015). A meta-analysis in European temperate forests found that vascular plants tend to have higher species richness in managed forests whereas bryophytes have higher species richness in unmanaged forests (Paillet et al., 2010). Management can also affect species composition; differences in floristic composition have been reported between managed and unmanaged forests both for vascular plants (Burrascano et al., 2008) and for bryophytes (Hofmeister et al., 2015).

Studying the effects of forest management history in Europe is complicated by the fact that all forests have been impacted by humans in some way. Consequently, the forests described as managed and unmanaged in different local studies may comprise highly variable management histories. For instance, managed stands differ widely in what kind of management has been done, how intensive it has been and how much time has passed since the last intervention. Currently unmanaged stands, in turn, may have been managed in the past, so some of their features may still reflect past management regimes and be dependent on the time lapse since management ceased. Therefore, general comparisons are context-sensitive, although it can be generally assumed that the more intensive the management, the larger the differences between managed and unmanaged forests (Stephens and Wagner, 2007; Horvat et al., 2017a, b).

Vascular plants and bryophytes differ in several fundamental traits, including the pathways of nutrient and water uptake (Cornelissen et al., 2007), so they may also respond differently to environmental factors (Bacaro et al., 2008), including forest management. If so, they would provide complementary data for management effect assessment (Økland et al., 2004; Lalanne et al., 2010). The prevailing view is that bryophytes are more sensitive to forest management than vascular plants (Kantvilas et al., 2015). In particular, bryophytes respond to forest structural features, such as the quantity of dead wood (Ódor and Standovár, 2001; Müller et al., 2015), which may be irrelevant for vascular plants. Due to such differences, inferences may not be generalizable from vascular plants to bryophytes or vice versa (Bagella, 2014), so comparing these plant groups in managed and unmanaged stands may provide valuable information about forest functioning.

Bryophytes have been little studied in temperate forests (Müller et al., 2015) and cross-taxon analyses between bryophytes and vascular plant studies are also rare (Bagella, 2014). The present study contributes to cross-taxon understanding in the western Pyrenean silver fir–beech forests. Previous studies have assessed the relationships of forest management and plant diversity in these forests, both for vascular plants (Horvat et al., 2017a) and for bryophytes (Delgado and Ederra, 2013; Iglesias et al., 2015; Horvat et al., 2017b), but these two functional groups have not been analytically compared. It has recently been found that decrease in vascular plant species richness was related to cessation of forest management (Horvat et al., 2017a), whereas decrease in bryophyte species richness was related to intensive management (Horvat et al., 2017b). However, the potential effect of stand structure on the diversities of these plant groups has not been analysed yet.

The present study compares the effect of forest management on two plant groups, bryophytes and vascular plants, by analysing data from managed and unmanaged silver fir–beech forests in the western Pyrenees. We provide a detailed environmental characterization of these mixed mountain forests and assess how structural, edaphic and climatic environmental drivers may affect the diversity of vascular plants and bryophytes. To obtain more detailed insight into the question, we split both plant groups into smaller species groups according to habitat preference and life strategy . On the basis of previous studies (Horvat et al., 2017a, b; Paillet et al., 2010), we expected that the two plant groups would respond differently to environmental predictors. We also expected differences in species diversity between managed and unmanaged stands. Specifically, we aim to clarify 1) the relative importance of environmental factors in explaining species richness and species turnover patterns of vascular plants and bryophytes, 2) whether forest management history itself has additional explanatory power, and 3) whether the compositional patterns of the two plant groups are congruent.

2. MATERIAL AND METHODS

2.1. Study area

The study area is located in the Spanish part of the western Pyrenees, in the regions of Navarre and Aragón (Fig. 1). The landscape is characterised by mountains and valleys with bedrock formed by limestones and marly flysch. Biogeographically, this area belongs to the Alpine Region and the bioclimate is characterised as temperate oceanic in the Global Bioclimatic Clas-

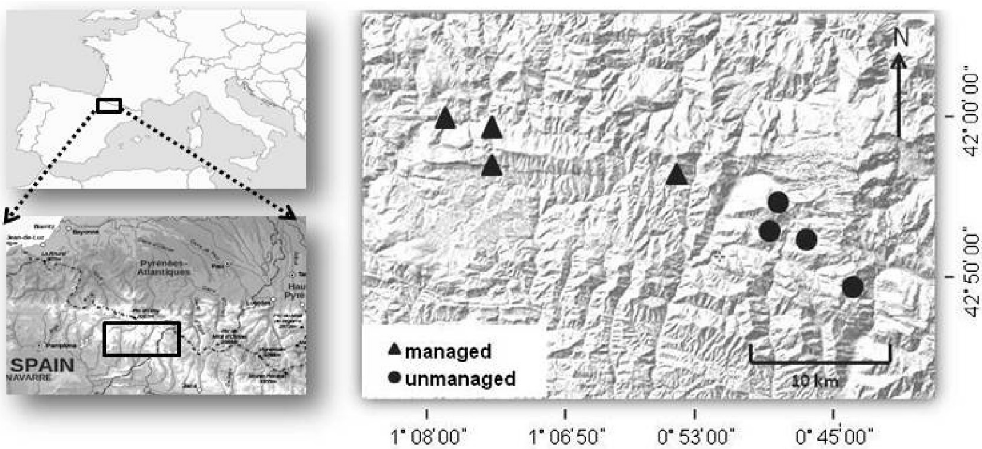

Fig. 1. Study area and location of the eight sampled stands in the western Pyrenees, provinces of Navarre and Aragón, N Spain.

sification System developed by Rivas-Martínez (2007). Mean annual temperature is 8°C, mean annual rainfall is 1419 mm and continentality increases gradually from west to east. A long history of livestock grazing and forest exploitation has shaped the landscape in this area, which is highly heterogeneous and contains semi-natural grasslands, scrublands, natural forests and *Pinus sylvestris* plantations.

The silver fir–beech forests of the study area are included in the association *Scillo lilio-hyacinthi-Fagetum sylvaticae* Br.-Bl. ex O. Bolòs 1957, which encompasses omprophilous hyperhumid forests growing on calcareous bedrock (Rivas-Martínez et al., 1991), from the suballiance *Scillo-Fagenion* (Willner et al., 2017). The long-term management history of these stands is unknown, because silvicultural practices with different intensities have been conducted unsystematically during the last century. A high variety of management types have been documented, including group selection logging, shelterwood, selective logging and exclusive fir exploitation. In general, the westernmost stands within the study area have been managed recently and also have active management plans, whereas the easternmost stands have not been managed for at least 40 years and they currently belong to natural parks and strictly protected reserves.

2.2. Sampling design

Our study was focused on north-facing stands of silver fir–beech forests that exceeded 30 ha in area and were situated in an altitudinal range between 800 and 1,700 m above sea level. Twenty stands fulfilling these criteria were identified using maps of potential vegetation and aerial photographs provided by the Governments of the provinces Navarre and Aragón. Field work was carried out in managed and unmanaged stands (Appendix A) selected based on our previous knowledge about management in this area (Horvat et al., 2017a). As *managed* we considered recently managed stands (active management interventions have taken place 5 to 20 years ago), whilst as *unmanaged* we considered the stands in which timber harvesting or any other intervention has not occurred for more than 40 years. A nested sampling design was used, in which management was set as a fixed factor with two levels. Within each management level, four stands were chosen, and within each stand four plots of 20 m × 20 m were randomly sampled. This gave a total of 32 plots in eight clusters (Fig. 1). The rarity of unmanaged forests in the western Pyrenees did not allow us to sample more stands. The presence of vascular plant and bryophyte species, stand structure, light regime and soil properties were recorded in each plot. Field sampling was carried out during summers of 2013, 2014 and 2015 with permits of the Government of Navarre and Aragon.

Bryophytes were collected from all available substrates (soil, rocks, tree bark and dead wood), because bryophyte diversity patterns are intimately linked with habitat heterogeneity (Newmaster et al., 2005). Sampling effort was similar in each plot in terms of time spent censusing and the quantity of collected material. All the specimens recognized as morphologically different were kept in marked envelopes for further identification in the laboratory.

Vascular plant species nomenclature follows *Flora iberica* (Castroviejo, 1986-2013), except for *Asteraceae, Geraniaceae,* and *Poaceae*, which follow *Flora Europaea* (Tutin et al., 1968–1980). Bryophyte species nomenclature follows Ros et al. (2013) for mosses and Ros et al. (2007) for liverworts.

Stand structure sampling was based on measuring diameter-at-breast-height (DBH) for all trees within three concentric circles with radii of 4, 13, and 20 m. In each concentric circle, we recorded all standing trees (living and dead) exceeding a pre-established diameter (DBH) threshold, which was 2.5 cm for the 4-m radius circle, 10 cm for the 13-m radius circle, and 50 cm for the 20-m radius circle. The trees with diameter exceeding 40 cm were considered large trees. For the dead standing trees, we use the term snags. For dead wood quantification, the diameter of all the lying dead wood components (logs) with minimum diameter ≥ 10 cm was recorded within the 13-m radius circle. To express structural diversity, the coefficient of variation of the diameter distribution (*VarD*) according to Sterba and Zingg (2006) was calculated for each plot. *VarD* is a distance-independent indicator of the vertical structure of a forest stand calculated as follows: $VarD = 100 \times sdDBH/xDBH$ where sdDBH is standard deviation of the DBH classes and xDBH is mean DBH.

Variables of light conditions (Table 1) were obtained by hemispherical photography. A detailed protocol of light sampling and analysis is described in Horvat et al. (2017a). We calculated the following variables: *transmission*, which is a measure of overall canopy openness or total gap fraction within the defined rings, including both small and large gaps; *gaps*, the proportion of large between-crown gaps estimated according to Chen and Cihlar (1995); and *LAI* (Leaf Area Index).

Climatic data (Table 1) were derived from digital maps (Ninyerola et al., 2005). We used mean annual temperature (T), total annual rainfall (P) and three bioclimatic variables (Rivas-Martínez, 2007): thermicity index (It), continentality index (Ic) and ombrothermic index (Io). These were calculated as follows: $It = (T+M+m) \times 10$, where M is average maximum temperature of the coldest month of the year and m is average minimum temperature of the coldest month of the year. $Ic = Tmax–Tmin$, where Tmax is mean temperature of the warmest month and Tmin is mean temperature of the coldest month. $Io = (Pp/Tp) \times 10$, where Pp is yearly positive precipitation in mm, i.e. total average precipitation of those months with an average temperature higher than 0ºC and Tp is yearly positive temperature, which is the sum of the positive monthly mean temperatures, in Celsius degrees.

Four topsoil cores (from the surface to10 cm depth) were randomly taken within each plot. All topsoil cores were pooled together to obtain one composite sample per plot, which was used for soil texture analysis and analysis of nutrients (Agro-environmental laboratory Fraisoro, Zizurkil). Soil texture analysis followed ISSS (International Society of Soil Science) criteria; nutrient analyses followed ADAS standard procedures (Jackson et al., 1986), except the nitrogen Kjeldahl, which, together with organic matter, was analysed following methods of MAFF (Ministry of Agriculture, Fisheries and Food, Spain). All environmental variables are listed in Table 1.

2.3. Data analysis

2.3.1. Species classification and general data exploration

Vascular plant species were categorized following Schmidt et al. (2011) and classified based of the information contained in the Vegetation-Plot Database of the University of the Basque Country, BIOVEG (EU-00-011; Biurrun et al., 2012) and of the available reference list about beech forest specialists (Willner et al., 2009). Two ecological groups were distinguished: forest specialists (FS), species largely restricted to closed forests, and non-forest species (NF) which included forest edge species, generalists and open area species.

Bryophytes were classified according to their life-strategy type (Dierssen, 2001) into short-lived (SL) and long-lived (LL) species. The category short-lived includes fugitives, annual shuttles, colonists, ephemeral colonists, pioneer colonists, short-lived shuttles and geophytes, and the category long-lived includes long-lived shuttles, competitive perennials, stress tolerant perennials and dominant perennials. All observed bryophytes were identified to species level, except some specimens of the genus *Ulota*: only specimens with a developed capsule were identified to species level, otherwise (in 11 plots) they were identified to genus level only. Spe-

Table 1. Environmental variables available for 32 plots used in the analyses of plant species diversity in the western Pyrenean silver fir–beech forests. Differences between managed and unmanaged stands were tested using Mann-Whitney's U test. * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$.

Variables	Unit	Managed Mean±SD	Unmanaged Mean±SD	*p* value
Topography				
Elevation	m a.s.l.	1118±104.70	1447±140.76	5.096e-06***
Slope	%	46.62±16.21	39.19±12.40	0.19
Light conditions				
Transmission	%	10.81±6.13	11.20±2.67	0.36
Gaps	%	6.7±5.50	5.9±2.28	0.89
LAI		4.28±0.96	4.04±0.79	0.54
Climate				
(T) mean annual temperature	°C	9.46±0.32	7.95±0.49	1.07e-06***
(P) annual rainfall (mm)	mm	1422±73.39	1384±72.33	0.28
(It) thermicity index		137.6±11.03	89.73±13.62	1.383e-06***
(Ic) continentality index		15.95±0.42	16.51±0.40	0.0002***
(Io) ombrothermic index		12.63±0.98	14.15±1.10	0.0015***
Soil				
pH (1:2,5 V/V)		5.4±0.37	5.7±0.33	0.02*
Coarse sand (0.2-2.0 mm)	%	2.35±0.95	4.95±2.42	0.002**
Fine sand (0.002-0.2 mm)	%	21.95±6.14	29.63±8.08	0.006**
Clay (< 0.002 mm)	%	32.91±3.55	29.76±5.85	0.05
Silt (0.002-0.02 mm)	%	42.80±4.91	35.94±5.06	0.0003***
Organic matter	%	7.62±2.11	7.94±2.01	0.61
Nitrogen Kjeldahl	%	0.27±0.03	0.63±0.11	0.01*
Phosphorus	mg/l	3.31±0.94	3.96±1.69	0.38
Potassium	mg/l	88.31±25.22	69.31±16.09	0.004**
Calcium	mg/l	1459.8±1135.09	1336.4±484.2	0.73
Sodium	mg/l	8.43±2.85	6.18±2.42	0.02*
Magnesium	mg/l	101.62±44.93	86.69±32.12	0.27
Aluminium saturation (Al%)	%	15.01±20.66	5.26±10.46	0.06
Stand structure				
Tree density	(N/ha)	638±286	806±617	0.83
Basal area of living trees	(m^2/ha)	34.95±9.41	35.20±12.61	0.79
Basal area snags	(m^2/ha)	1.21±2.47	2.27±2.75	0.06
Basal area logs	(m^2/ha)	3.89±3.91	2.21±1.80	0.46
Total basal area of dead wood	(m^2/ha)	5.09±4.18	4.53±2.77	0.95
Number of large trees	(N/ha)	84.29±29.61	88.77±41.85	0.83
Number of large fir trees	(N/ha)	39.49±35.20	32.80±41.85	0.35
Number of large beech trees	(N/ha)	45.29±31.67	55.97±33.85	0.35
VarD		50.40±18.23	62.36±17.77	0.06

* CEC - cation exchange capacity

cies-level identifications (*Ulota crispa, U. bruchii* and *U. crispula*) were used in the general species lists, but for the quantitative numerical analyses we used genus-level identifications (*Ulota* sp.)

Differences between the two management categories in stand structure, climatic conditions and soil properties were assessed by the Mann-Whitney's U test.

2.3.2. Species richness

Generalized linear mixed models were used to determine which environmental variables best explain variation in species richness of all plants, vascular plants and bryophytes, as well as of the ecologically defined subgroups (FS, NF, SL and LL). Environmental variables were taken as fixed effects, and stand, which was nested within management type, was considered as a random effect. Poisson error distribution for count data and log link function were used. Environmental variables were standardized to zero mean and unit variance, and Spearman correlation analysis was performed among them to detect collinearity. Drivers of species richness were assessed using multimodel inference. The full model and all possible sub-models were fitted according to Information-Theoretic (IT) approach (Burnham and Anderson, 2002) using *dredge* function in *MuMIn* package in R. Models were ranked based on their AICc, which is a criterion used as a measure of model quality for small sample sizes. The best fitting sub-models, i.e. those within a distance of 2 AICc units from the first ranking model, were tested for overdispersion. We also tested whether the residuals of any model showed significant spatial autocorrelation using the *ape* package in R, but they did not (results not shown). To assess the magnitude of a possible management effect, we calculated the log response ratio, a metric that expresses proportional differences in species richness between managed and unmanaged stands. Effect sizes of other variables were displayed using the *effects* package in R.

2.3.3. Species turnover

To assess which factors explain variation in species turnover, we opted for a distance-based variation partitioning approach. This was done both because pairwise dissimilarity indices provide a natural measure for species turnover, and because a distance-based approach allows directly incorporating geographical distances into the models. By variation partitioning, we quantified the contribution of environmental differences and geographical distances to explaining species turnover, which helps to separate between the effects of dispersal limitation and of species responses to spatially autocorrelated environmental variables (Tuomisto and Ruokolainen, 2005; Lichstein, 2007; Sabatini et al., 2014). The response variable, species turnover, was calculated using the Sørensen dissimilarity measure (calculated as the one-complement of the Sørensen similarity index that expresses the number of shared species as a proportion of the mean number of species in the plots being compared). Separate analyses were run for species turnover of all plants, vascular plants and bryophytes. The explanatory variables were dissimilarity matrices calculated for each environmental variable separately using the Euclidean distance, and a matrix of straight-line geographical distances. For each plant group, we first ran a set of simple Mantel tests (999 permutations) using each explanatory variable separately. All the variables that returned a significant Mantel test result were then used in Multiple Regression on Distance Matrices (MRM), which was simplified by backward elimination to retain only those explanatory variables that had a significant partial contribution to the final model. The contribution of each variable on its own and in combination with the other variables to explaining variation in species turnover was then quantified by running a series of MRM models using different subsets of the retained explanatory variables.

The differences in species composition among plots were visualised, for each plant group separately, with NMDS ordination (non-metric multidimensional scaling) based on the Sørensen dissimilarity matrices. To find a stable solution, 500 NMDS ordinations with random starting configurations were run in each case. The environmental variables retained in the final MRM model were then passively projected on the corresponding ordination diagram. Finally, the correspondence between vascular plant and bryophyte species turnovers was quantified using a Mantel test. Multivariate analyses were performed with *vegan* and *ecodist* packages in R. All analyses were run using (v. 3.2-5) R statistical environment (R Foundation for Statistical Computing, Vienna, AT).

3. RESULTS

3.1. Overall floristic results

In the overall floristic survey of 32 plots, we identified 155 plant species, including 93 vascular plants, 51 mosses and 11 liverworts (Appendix B). Managed stands had more species than unmanaged forests, both for vascular plants and for bryophytes (Table 2). Mean total species richness (± standard deviation) per plot was 28.7 ± 12.3. The mean vascular plant richness was 17.5 ± 10.2 species per plot, varying from 4 to 44 species in the individual plots. Shrub layer was sparse, and it consisted mostly of juvenile *Fagus sylvatica* occurring in the gaps and a few individuals of *Daphne laureola*. Herb layer was mainly formed by forest specialists (61 % of the species). The most frequent herbaceous vascular species were: *Carex sylvatica* (in 81 % of the plots), *Veronica montana* (68 %), *Athyrium filix-femina* (62 %) and *Oxalis acetosella* (59 %). Twenty-seven vascular plant species (29%) occurred in only one plot. The mean bryophyte richness was 11.62 ± 6.09 species per plot, ranging from 3 to 26 species in the individual plots. The plot with only three bryophyte species had very dense beech regeneration and seemed to lack suitable microhabitats for bryophytes. The most frequent bryophytes were *Brachythecium velutinum* var. *velutinum* (in 72 % of the plots), *Pterigynandrum filiforme* var. *filiforme* (72 %), *Isothecium alopecuroides* (62 %) and *Atrichum undulatum* (56 %). Twenty-one bryophyte species (33 %) occurred in only one plot, and some of these were rare and protected species such as *Dicranodontium denudatum* and *Orthotrichum shawii*. The latter is included in the Spanish Red List of bryophytes and categorized as "Vulnerable" (Garilleti and Albertos, 2012). Regarding bryophyte life-strategy, we found 20 *short-lived* bryophyte species (32 % of the species) and 42 *long-lived* species (67 %) (Appendix B).

3.2. Environmental variability

Tree layer was dominated by beech, followed by silver fir. Regarding forest structural variables, managed and unmanaged stands did not show significant differences (Table 1). *Transmission*, an overall canopy openness, and *gaps,* percentage of large gaps, were highly correlated (r=0.92). *Transmission* average was 11.1%, whilst the *gaps* average was 6.34%, thus percentage of large gaps describe more than half of overall canopy openness. No significant difference between management categories regarding the percentage of large gaps was found (Table 1).

Soil texture and nutrient content varied across stands and plots. Soil texture was classified as clay loam in 22 plots, as silt in five and as silt loam in five. Managed stands had higher silt percentages as well as potassium and sodium contents, whereas unmanaged stands had higher pH, nitrogen content and percentage of fine and coarse sand (Table 1). The 40 km of E-W distance was sufficient for the climatic conditions to differ over the study area (Table 1). Managed stands were located in the western part of study area, which corresponded to lower elevations

Table 2. General floristic data of managed and unmanaged stands in silver fir–beech forests from the western Pyrenees. FS, forest specialists; NF, non-forest species; SL, short lived bryophytes; LL, long-lived bryophytes. Differences between managed and unmanaged stands were tested using Mann-Whitney's U test. * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$.

	Managed Mean±SD	Unmanaged Mean±SD	*p* value
Total species richness	134	94	-
Vascular plant richness	83	55	-
Bryophyte richness	54	38	-
Mean plant species richness	34.81±13.97	22.56±5.98	0.01**
Mean vascular plant richness	20.93±12.75	14.00±5.29	0.18
Mean FS richness	15.37±8.72	9.18±3.29	0.20
Mean NF richness	5.25±4.52	2.50±1.82	0.07
Mean bryophyte richness	14.18±7.23	9.06±3.25	0.14
Mean SL richness	3.37±2.47	2.56±1.15	0.01**
Mean LL richness	10.87±5.45	6.37±2.44	0.10

with higher mean annual temperature and thermicity index. Conversely, unmanaged stands were concentrated in the eastern part, on higher elevations, and showed significantly higher continentality and ombrothermic index (Table 1).

3.3. Drivers of species richness

GLMM modelling showed that total species richness was best explained by *gaps* (positively correlated with species richness), soil silt content and elevation (both negatively correlated; Table 3). Due to the spatially clustered sampling setup, elevation and management type were highly correlated. If entered separately into the model, both variables were significant, but the model using elevation as predictor had a slightly better fit and is therefore shown in Table 3. Effects of the significant variables were generally weak (Fig. 1C, Fig. 2C and Fig. 3C in Appendix C).

Vascular plant and non-forest species richness followed the same pattern as total species richness, whilst forest specialist richness was not explainable by any of the predictor variables. Total bryophyte richness was negatively correlated with elevation, but in this case aluminium saturation emerged as a significant variable whereas gaps and silt were not significant (Table 3, Fig. C4 in Appendix C). However, the explanatory power of aluminium saturation was weak, and it was not significant for any of the bryophyte subgroups. Elevation was negatively correlated with richness of short-lived bryophytes, whilst richness of long-lived bryophytes did not respond to any of the predictor variables (Table 3).

3.4. Species turnover

In multiple regression on distance matrices, 24.8% of the variation in the species turnover of all plants could be explained with geographical distances and differences in aluminium saturation, *gaps* and number of large fir trees (Fig. 2). The unique contribution of geographical distances to explaining the variance (12.7%) was higher than the unique contribution of the three environmental variables taken together (9.7%). The fraction that was shared between geographical and environmental distances was small (2.5%). The unique contributions of the three environmental factors separately ranged from 3.1 to 4.1%.

Table 3. Summary results of GLMM models explaining total plant species richness and richness of species in different ecologically defined plant groups with stand properties. Poisson error distribution for count data and log link function were used. Stand was included as a random factor, nested within management category. * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$.

Total plant species richness ~ silt + gaps + elevation + (1 | stand)

	Estimate	Std.error	z value	Pr(>|z|)
(intercept)	3.32118	0.06435	51.61	< 2e-16***
Silt	-0.0127	0.04985	-2.57	0.01029*
Elevation	-0.3098	0.06506	-4.76	1.91e-06***
Gaps	0.1258	0.03452	3.64	0.00026***

Vascular plant richness ~ silt + gaps +elevation + (1 | stand)

	Estimate	Std.error	z value	Pr(>|z|)
(intercept)	2.75066	0.11172	24.621	< 2e-16***
Silt	-0.0213	0.06279	-3.408	0.00065***
Elevation	-0.2766	0.09996	-2.768	0.00564**
Gaps	0.1336	0.4311	3.099	0.00193**

Non-forest species richness ~ silt + gaps + elevation + (1|stand)

	Estimate	Std.error	z value	Pr(>|z|)
(intercept)	1.10937	0.11297	9.820	< 2e-16***
Silt	-0.5573	0.11314	-4.926	8.40e-07***
Elevation	-0.6476	0.15283	-0.428	2.26e-05***
Gaps	0.364	0.08121	4.483	7.37e-06***

Bryophyte richness ~ aluminium + elevation + (1| stand)

	Estimate	Std.error	z value	Pr(>|z|)
(Intercept)	2.38581	0.12388	19.260	< 2e-16***
Aluminium	-0.163	0.07587	-2.160	0.03077*
Elevation	-0.358	0.11376	-3.147	0.00165**

Short-lived bryophyte richness ~ elevation + (1 | stand)

	Estimate	Std.error	z value	Pr(>|z|)
(intercept)	0.08148	0.18155	0.449	0.65358
Elevation	-0.55889	0.18393	-3.039	0.00238**

In the case of vascular plant species turnover, MRM explained 17.4% of the variation with almost the same variables as for total plant species turnover (Fig. 2), although here difference in slope emerged as significant instead of difference in gaps. Contrary to the situation with all plants, for vascular plants most variation in species turnover was explained by the purely environmental fraction (13%), with the purely spatial fraction being only 2.2%.

Variance in bryophyte turnover was explained only by geographical distances and the model explained 15.6% (Fig. 2).

The NMDS ordinations showed that managed and unmanaged plots differed in species composition (Fig. 3). Main turnover drivers detected by MRM were passively projected on NMDS ordinations revealing that in the case of all plants species and vascular plants species none of the significant variables (gaps, number of large firs and aluminium percentage) were linked with management type (Fig. 3).

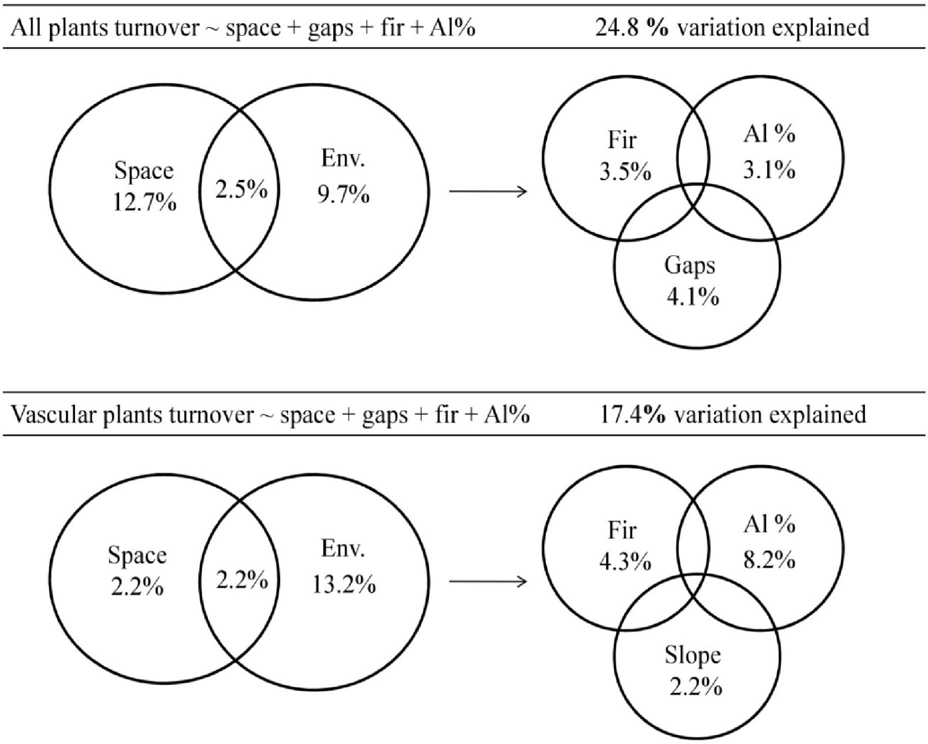

Fig. 2. Results of multiple regression on distance matrices (MRM) analysing the contributions of different factors to explaining variation in the turnover of all plant species, vascular plant species and bryophyte species in silver fir–beech stands in the western Pyrenees. Both unique and shared proportions of explained variance are shown for the significant variables. Explanatory matrices were based on differences in the following variables: space, geographical location (hence, the actual explanatory variable was geographical distance); Al%, aluminium saturation; gaps, percentage of large gaps; and fir, number of large fir trees per hectare.

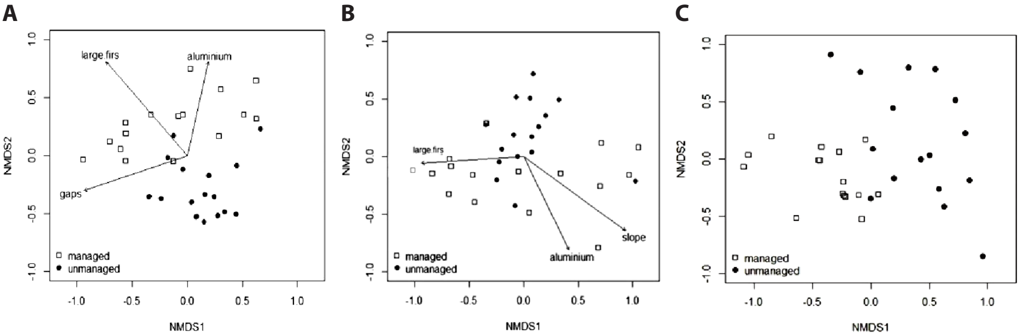

Fig. 3. Non-Metric Multidimensional scaling ordinations based on species turnover of all plant species (A), vascular plant species (B) and bryophyte species (C) in 32 plots in the silver fir–beech forests from the western Pyrenees. Species turnover was quantified using the Sørensen dissimilarity index. Vectors represent the correlations between the ordination axes and the environmental variables that were found significant in MRM analysis.

Finally, the Mantel test indicated that the correlation between vascular plant and bryophyte species turnovers was not statistically significant (r=0.12; *p*=0.088).

4. DISCUSSION

4.1. Species richness

In our analyses of western Pyrenean silver fir–beech forests, stand structure did not play any role in explaining plant species diversity. This is in agreement with recent results obtained in the Apennine beech forests (Sabatini et al., 2016), but several other studies have highlighted the effect of forest structure on plant species diversity (Barbier et al., 2008, 2009; Abbate et al., 2015). The lack of correlation in our data may be due to stand structure being rather similar in the managed and unmanaged forests. In addition, past management and other disturbances may have affected biodiversity in ways that are not detectable by forest structure measurements (Gossner et al., 2014).

According to our results, elevation explained variation in species richness best, although its effect was not very clear and forest management was almost as good predictor as elevation. However, elevation and forest management have a similar spatial structure in our data, and their covariance makes it impossible to statistically separate their effects. On a theoretical basis, both elevation and forest management could be expected to affect vascular plant and bryophyte species richness (Vittoz et al., 2010; Müller et al., 2015).

Our results identified soil silt content as potentially important explanatory factor for the species richness of vascular plants, but not for bryophytes. We observed negative relation between vascular plant species richness and soil silt content, which is in agreement with reports from Hungarian forests (Márialigeti et al., 2016). Such soils with higher silt percentage are associated with low infiltrability (Mills and Macdonald, 2004) and poorer water conditions (Márialigeti et al., 2016), which is not favourable to herb cover. Lower soil infiltrability may affect plant growth, nutrient uptake and therefore vascular species richness, since not all the species are adapted to such conditions. Clay also has a similar effect on vascular plants, but its percentage in soil does not differ among stands, hence the silt is driving soil impermeability. This is not a case for ground-dwelling bryophytes which use the ground surface as substratum and may compensate humidity needs from the air.

The percentage of large gaps was positively related to total species richness and vascular plant richness, but not to bryophyte richness. Hence, gaps effect on total species richness can be attributed to their effect on vascular plant richness. In the sampled stands, larger gaps drove to higher vascular plant species richness both in managed stands, where gaps are consequence of logging, and in unmanaged stands, where gaps remain large because of natural disturbances. Higher light levels might cause the entrance of non-forests species. In fact, their richness also increased with the percentage of large gaps, and the magnitude of the effect was even stronger as they are light-demanding. In contrast, bryophyte species richness was not affected by large gaps. The absence of light effect on bryophyte richness might be due to the presence of microhabitats, which could mitigate differences in light levels; in the case that plots have higher light levels, bryophyte richness still could be high if there are enough microhabitats on which bryophyte richness highly depends (von Oheimb et al., 2007).

Bryophyte species richness was correlated with soil aluminium saturation, but there are only three terricolous bryophytes in our species pool which could be directly affected by this soil property. Therefore, this result is unlikely to be causal, but instead reflects covariation with some other variable, such as soil pH.

The obtained results suggest that the species richness patterns of vascular plants and bryophytes differ in their environmental relationships within the silver fir–beech forests from the western Pyrenees. This is in line with earlier result about divergent plant species richness patterns in a large range of cases in different habitats and locations (Dirkse and Martakis; 1998; Molau and Alatalo, 1998; Bagella, 2014). For instance, Pausas (1994) reported that in *Pinus sylvestris* forests of the eastern Pyrenees, species richness of vascular plants was mostly affected by radiation whereas that of bryophytes was more related to moisture and soil pH. Indeed, Bagella (2014) concluded that vascular plants cannot be considered a good surrogate for bryophyte richness patterns, because the two plant groups respond differently to environmental factors. According to Bagella (2014), in mountain areas bryophyte richness showed a more gradual decrease in species richness with increased elevation than vascular plants, as the bryophytes are more humidity depended than vascular plants. The response of these two taxonomic groups to forest management was heterogeneous and still is not possible to drive general conclusions (Bagella, 2014).

4.2. Species turnover

In our data from the western Pyrenean forests, the predictors of plant species turnover retained by multiple regression were related to both geographical distances and environmental heterogeneity. The largest part of variation was uniquely explained by geographical distances for all plants, but bryophytes showed clearly stronger decay of floristic similarity with increasing geographical distance than vascular plants did. Bryophytes are considered well-dispersed organisms (Mikulášková et al., 2015) and it is unlikely that wind-dispersed bryophytes would be more dispersal limited than seed plants. Therefore, variation in bryophyte turnover might partly be related to some unmeasured environmental variables that are themselves spatially autocorrelated. Although we measured many potentially relevant variables at the plot level, within-plot variability was not documented in our random sampling. Potentially important unmeasured variables include different aspects of microhabitat. However, their spatial clustering might also reflect the existence of dispersal limitation (Löbel et al., 2006). This aggregated distribution patterns of bryophytes may occur because of unsuitable habitat for spores to germinate (Hassel et al., 2005). Barbé et al. (2016) highlight that sexual organ production and microhabitat availability may be more limiting than dispersal capacity for bryophyte metacommunity assemblages. For instance, many bryophytes have restricted distribution ranges depending on the availability of suitable habitats such as dead wood (Ódor and Standovár, 2001) which is a spatially discontinuous habitat. Despite these observations, the spatial clustering of some bryophytes might be attributed to their distribution area, for instance *Frullania tamarisci*, *Isothecium mysuroides* subsp. *myosuroides*, *Neckera pumila* and *Thuidium tamariscinum*, found in the westernmost stands, are more frequent under the stronger Atlantic influence (Lecointe, 1980; De Miguel and Ederra, 1984; Heras, 1985). Conversely, *Dicranum tauricum* occurred only in the eastern part of the study area, which may be due to its affinity to high continentality. The possible effects of these climatic differences are difficult to statistically separate from those of geographical distance in our data.

The percentage of large gaps was one of the environmental factors that emerged important in explaining total plant species turnover. Testing vascular plant and bryophyte species turnover separately, the percentage of large gaps was a significant predictor only in the case of vascular plants. This can be interpreted to affect the occurrence of light-demanding species in the case of vascular plants, but not in the case of bryophytes. The plots with higher percentage of large gaps (>8%) contained some non-forest vascular species, such as *Rubus* sp. pl., *Juncus effusus*, *Taraxacum officinale*, *Atropa bella donna* and *Digitalis purpurea*. The same observation that vascular plant turnover is caused by light regime is reported in Hungarian forests (Tinya and Ódor, 2016). For instance, bryophyte species with different light sensibilities (following Dierssen, 2001) were found in the same plot.

Soil aluminium saturation did not explain vascular plant species richness, but it was the most important predictor of vascular plant species turnover. High aluminium saturation is actually an indication of low soil pH, and the plots with the highest aluminium saturation and lowest pH values contained some acidophilic species such as *Vaccinium myrtillus, Deschampsia flexuosa* and *Ilex aquifolium.*

The between-plot differences in number of large fir trees partly explained vascular plant species turnover. The presence of large fir trees might provide different microclimatic conditions on the plot-scale. As an evergreen species, fir trees maintain stable light conditions throughout the year, as they create shady conditions also during winter months. On such permanent shadow during all the year certain species may show preference. The variation in large fir trees presence in the studied area might be linked with former intensive forest management (Camarero et al., 2011) which was oriented to logging the largest fir trees (Sangüesa-Barreda et al., 2015).

Analyzing different aspects of plant diversity in the western Pyrenean silver fir–beech forests our main result is that vascular plants and bryophytes appear to respond differently to environmental factors. Due to a lack of congruency in some results further research on this topic is needed and our study is a contribution to better understanding of variation in species richness of these two different taxonomic groups. As the vascular plants and bryophytes species turnovers were not correlated they should be analysed separately to have better insight into forest functioning.

ACKNOWLEDGEMENTS

We thank Daniel García Magro, Jorge García de Vicuña, Almudena Pereda Romero and Raul Ilundain for help in field sampling and Marta Infante for help in bryophyte identification. This manuscript was prepared during Vlatka Horvat's research visit to University of Turku; many thanks to all members of department of Biology for their warm welcome and hospitality.

Funds from the project IT299-10 for research groups of the Basque Government have been used for this survey.

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SUPPLEMENTARY MATERIAL

APPENDIX A. Characteristics of the sampled stands in the silver fir-beech forests from the western Pyrenees.

	Management category	Elevation (m a.s.l.)	Stand's coordinates (x,y)	Stand surface area (ha)
Lizardoia	managed	980-1080	0653820, 4763330	49
San Fermin	managed	1000-1230	0655930, 4761810	49
Eskalera	managed	990-1140	0654482, 4760315	30
Pikatua	managed	1110-1300	0661514, 4758615	32
Maze	unmanaged	1320-1520	0677288, 4751014	68
Aztaparreta	unmanaged	1600-1650	0677940, 4753194	93
Gamueta	unmanaged	1340-1530	0679985, 4750580	82
Selva de Oza	unmanaged	1200-1400	0686280, 4744519	32

APPENDIX B

Table B.1. Vascular plant species list in silver fir-beech forests in the western Pyrenees (FS, *forest specialist*; NF, *non forest species*).

	Vascular plant species	Frequency	Habitat preference
1	*Abies alba*	32	FS
2	*Acer opalus*	2	FS
3	*Adenostyles alliariae*	6	NF
4	*Agrostis capillaries*	5	NF
5	*Ajuga reptans*	3	NF
6	*Alchemilla* sp.	1	NF
7	*Anemone nemorosa*	1	FS
8	*Asplenium trichomanes*	1	NF
9	*Athyrium filix-femina*	20	FS
10	*Atropa bella donna*	1	NF
11	*Blechnum spicant*	5	FS
12	*Brachypodium pinnatum* subsp. *rupestre*	5	NF
13	*Brachypodium sylvaticum* subsp. *sylvaticum*	5	FS
14	*Cardamine flexuosa*	11	FS
15	*Cardamine heptaphylla*	10	FS
16	*Cardamine pentaphyllos*	4	FS
17	*Carex digitata*	1	FS
18	*Carex divulsa* subsp. *divulsa*	2	NF
19	*Carex muricata*	3	NF
20	*Carex remota*	3	FS
21	*Carex sylvatica*	26	FS
22	*Chrysosplenium oppositifolium*	3	FS
23	*Circaea lutetiana* subsp. *lutetiana*	1	FS
24	*Cirsium palustre*	1	NF
25	*Cynosurus cristatus*	1	NF
26	*Daphne laureola*	3	FS
27	*Descampsia flexuosa*	3	NF
28	*Digitalis purpurea*	1	NF
29	*Dryopteris affinis*	4	FS
30	*Dryopteris affinis* subsp. *borreri*	4	FS
31	*Dryopteris dilatata*	2	FS
32	*Dryopteris filix-mas*	15	FS
33	*Epilobium montanum*	8	FS
34	*Epipactis helleborine*	9	FS
35	*Euphorbia amygdaloides*	6	FS
36	*Fagus sylvatica*	32	FS
37	*Fragaria vesca*	11	NF
38	*Fraxinus excelsior*	5	FS
39	*Galium odoratum*	12	FS
40	*Galium rotundifolium*	1	FS
41	*Geranium robertianum*	11	NF
42	*Geum urbanum*	1	NF
43	*Gymnocarpium dryopteris*	8	FS
44	*Hedera helix*	2	NF
45	*Helleborus viridis* subsp. *occidentalis*	4	FS
46	*Hordelymus europaeus*	9	FS

Table B.1. (Cont.).

	Vascular plant species	Frequency	Habitat preference
47	*Hypericum androsaemum*	1	FS
48	*Ilex aquifolium*	5	FS
49	*Isopyrum thalictroides*	1	FS
50	*Juncus effuses*	3	NF
51	*Lamium galeobdolon*	8	FS
52	*Lathraea clandestine*	13	FS
53	*Luzula multiflora* subsp. *congesta*	1	FS
54	*Luzula pilosa*	3	FS
55	*Luzula sylvatica*	12	FS
56	*Lysimachia nemorum*	5	FS
57	*Melica uniflora*	3	FS
58	*Milium effusum*	10	FS
59	*Moehringia trinervia*	4	FS
60	*Monotropa hypopitys*	5	FS
61	*Mycelis muralis*	1	FS
62	*Neottia nidus-avis*	7	FS
63	*Oxalis acetosella*	19	FS
64	*Pinus sylvestris*	1	NF
65	*Poa nemoralis*	5	FS
66	*Polystichum aculeatum*	17	FS
67	*Potentilla sterilis*	4	FS
68	*Prenanthes purpurea*	1	FS
69	*Pteridium aquilinum* subsp. *aquilinum*	1	NF
70	*Quercus petraea*	1	FS
71	*Ranunculus repens*	1	NF
72	*Rosa arvensis*	1	FS
73	*Rubus* gr. *Hirtus*	1	NF
74	*Rubus idaeus*	3	NF
75	*Rubus* sec. *Corylifolii*	1	NF
76	*Rubus* sp.	6	NF
77	*Salix caprea*	1	NF
78	*Sambucus ebulus*	3	NF
79	*Saxifraga hirsuta* subsp. *hirsuta*	11	FS
80	*Scilla lilio-hyacinthus*	2	FS
81	*Scrophularia alpestris*	16	NF
82	*Sorbus aria*	1	FS
83	*Sorbus aucuparia*	14	NF
84	*Taraxacum officinale*	2	NF
85	*Ulmus glabra*	2	FS
86	*Urtica dioica*	3	NF
87	*Vaccinium myrtillus*	2	NF
88	*Veronica chamaedrys* subsp. *chamaedrys*	5	NF
89	*Veronica montana*	22	FS
90	*Veronica officinalis*	2	NF
91	*Veronica serpyllifolia*	1	NF
92	*Vicia sepium*	1	NF
93	*Viola reichenbachiana*	10	FS

Table B.2. Bryopyhte species list in silver fir-beech forests in the western Pyrenees (SL, short-lived bryopyhtes; LL, long-lived bryopyhtes)

	Bryopyhte species	**Frequency**	**Clade**	**Life-strategy**
1	*Antitrichia curtipendula*	10	moss	LL
2	*Atrichum undulatum*	18	moss	SL
3	*Blepharostoma trichophyllum* var. *trichophyllum*	2	liverwort	SL
4	*Brachythecium rutabulum*	10	moss	LL
5	*Brachythecium velutinum* var. *velutinum*	23	moss	LL
6	*Ptychostomum capillare*	3	moss	SL
7	*Ctenidium molluscum*	12	moss	LL
8	*Dicranodontium denudatum*	1	moss	LL
9	*Dicranum scoparium*	11	moss	LL
10	*Dicranum tauricum*	3	moss	LL
11	*Cirriphyllum crassinervium*	1	moss	LL
12	*Kindbergia praelonga* var. *praelonga*	1	moss	LL
13	*Eurhynchium praelongum* subsp. *stokesii*	1	moss	LL
14	*Eurhynchium pulchellum* var. *pulchellum*	1	moss	LL
15	*Oxyrrhynchium speciosum*	1	moss	LL
16	*Eurhynchium striatum*	8	moss	LL
17	*Fissidens taxifolius* subsp. *taxifolius*	11	moss	SL
18	*Fissidens viridulus* var. *viridulus*	1	moss	SL
19	*Frullania dilatata*	9	liverwort	LL
20	*Frullania fragilifolia*	3	liverwort	LL
21	*Frullania tamarisci*	6	liverwort	LL
22	*Herzogiella seligeri*	4	moss	LL
23	*Homalothecium lutescens* var. *lutescens*	1	moss	LL
24	*Homalothecium philippeanum*	1	moss	LL
25	*Hygrohypnum luridum*	1	moss	LL
26	*Hypnum cupressiforme* var. *cupressiforme*	17	moss	LL
27	*Isothecium alopecuroides*	20	moss	LL
28	*Isothecium myosuroides* subsp. *myosuroides*	9	moss	LL
29	*Lepidozia reptans*	2	liverwort	SL
30	*Lophocolea bidentata*	4	liverwort	LL
31	*Lophocolea heterophylla*	2	liverwort	SL
32	*Metzgeria furcata*	10	liverwort	LL
33	*Mnium hornum*	3	moss	LL
34	*Exsertotheca crispa*	2	moss	LL
35	*Neckera pumila*	9	moss	LL
36	*Orthotrichum affine*	1	moss	SL
37	*Orthotrichum lyellii*	13	moss	LL
38	*Orthotrichum shawii*	1	moss	SL
39	*Orthotrichum stramineum*	7	moss	SL
40	*Orthotrichum striatum*	10	moss	SL
41	*Plagiochila porelloides*	13	moss	LL
42	*Plagiomnium undulatum* var. *undulatum*	1	moss	LL
43	*Plagiothecium curvifolium*	1	moss	LL
44	*Plagiothecium nemorale*	2	moss	LL
45	*Plasteurhynchium striatulum*	1	moss	LL
46	*Pogonatum aloides*	1	moss	SL

Table B.2. (Cont.).

	Bryopyhte species	Frequency	Clade	Life-strategy
47	*Polytrichum formosum*	15	moss	LL
48	*Porella platyphylla*	9	liverwort	LL
49	*Pseudoleskea incurvata*	1	moss	LL
50	*Pseudotaxiphyllum elegans*	1	moss	SL
51	*Pterigynandrum filiforme* var. *filiforme*	23	liverwort	LL
52	*Radula complanata*	10	liverwort	LL
53	*Rhizomnium punctatum*	5	moss	LL
54	*Rhytidiadelphus triquetrus*	1	moss	LL
55	*Schistidium crassipilum*	5	moss	SL
56	*Syntrichia ruralis* var. *ruralis*	1	moss	SL
57	*Tetraphis pellucida*	1	moss	SL
58	*Thuidium tamariscinum*	12	moss	LL
59	*Tortella tortuosa* var. *tortuosa*	5	moss	LL
60	*Ulota bruchii*	7	moss	SL
61	*Ulota crispa*	2	moss	SL
62	*Ulota crispula*	1	moss	SL

APPENDIX C.

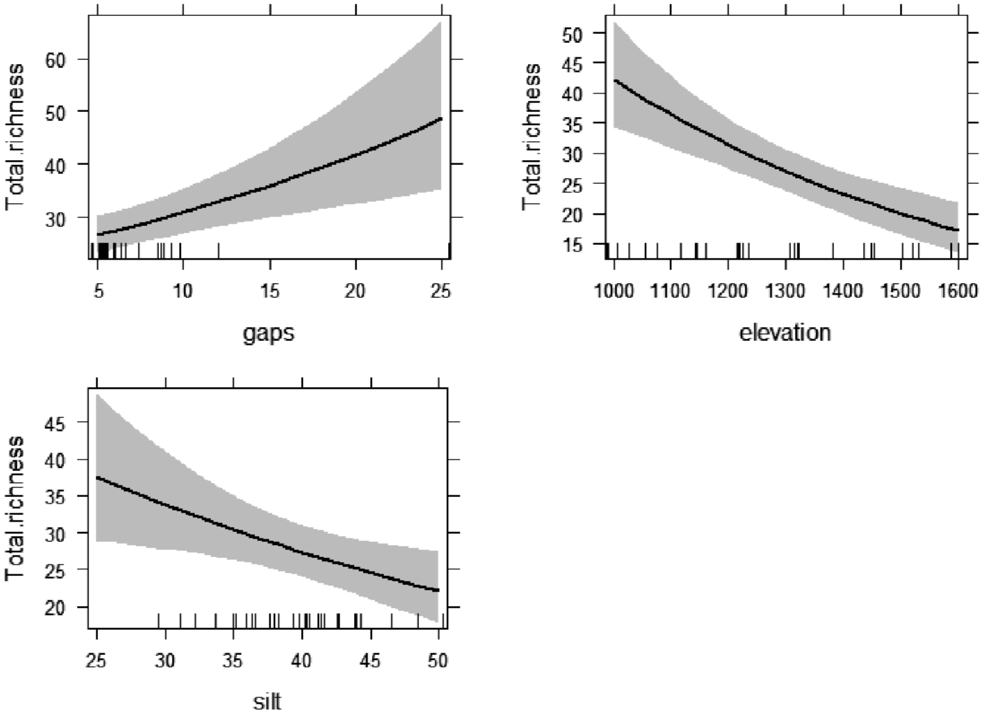

Fig. 1C. Model response of total species richness (vascular plants and bryophytes) to three significant variables (elevation, silt and gaps) as predicted by GLMMs model, with 95% confidence intervals. Vertical axis is displayed on the scale of the response.

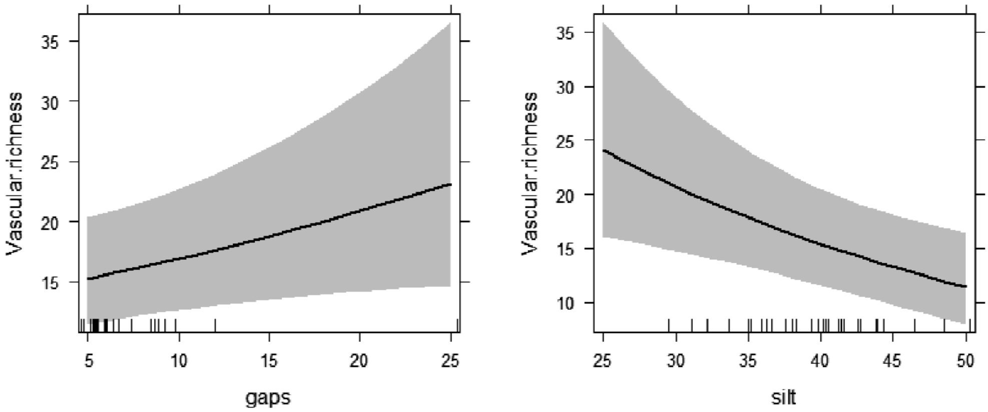

Fig. 2C. Model response of vascular plant species richness to two significant variables (silt and gaps) as predicted by GLMMs model, with 95% confidence intervals. Vertical axis is displayed on the scale of the response.

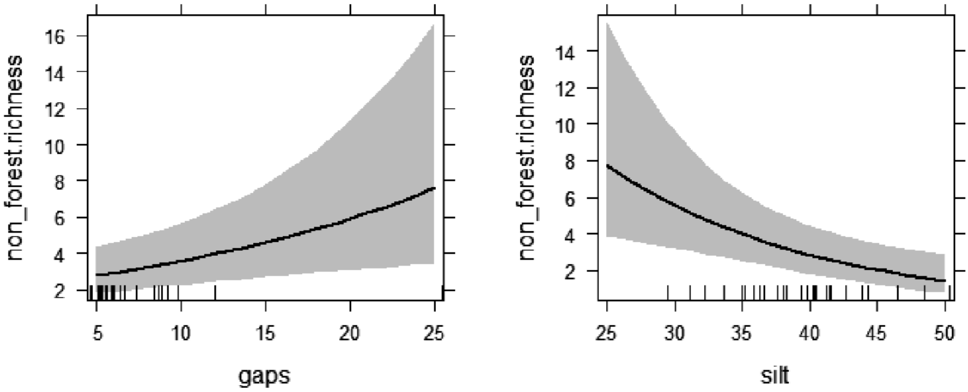

Fig. 3C. Model response of *non-forest* species richness to two significant variables, silt and gaps as predicted by GLM model, with 95% confidence intervals. Vertical axis is displayed on the scale of response.

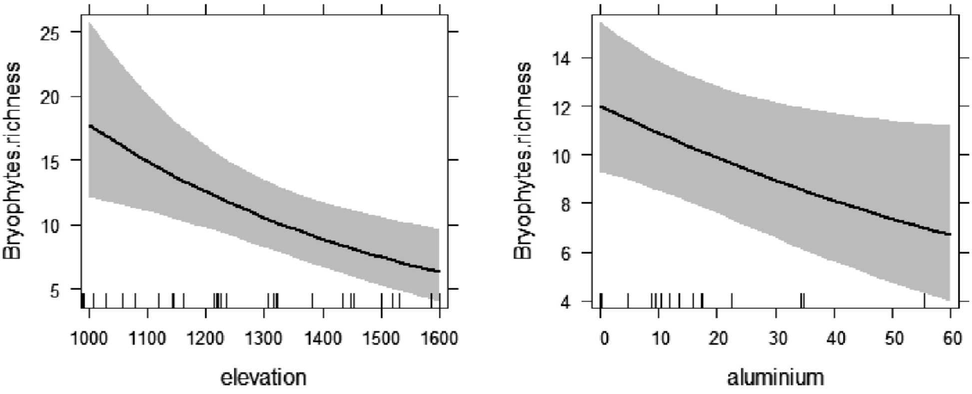

Fig. 4C. Model response of bryophytes richness species to aluminium saturation and elevation as predicted by GLMM model, with 95% confidence intervals. Vertical axis is displayed on the scale of response.

chapter 6

Vlatka Horvat (2018) PhD THESIS pp. 125-145

Evaluating lichen diversity as indicator of forest management: the role of rare species in the western Pyrenean silver fir–beech forests

ABSTRACT

Lichens are known to be sensitive to habitat disturbance and as such, some have been used as indicators of forest management. The influence of forest management on lichen diversity was studied for the first time in western Pyrenean silver fir–beech forests. Our specific aims were to determine the main drivers of lichen species richness and turnover and explore which lichens can be used as indicators of management intensity. The effect of management was assessed on the overall lichen diversity as well as on the lichen groups based on life-form, photobiont type, and lichen rarity. Lichen diversity was analysed by generalized linear mixed models and multiple regression analysis on distance matrices. In the overall survey of 32 plots, we identified 66 lichen and lichenicolous fungi species. Total lichen richness in Pyrenean forests decreased on the steeper slopes, which may be due to lichen exposure to higher light and wind levels. Fruticose and rare lichen richness was driven by elevation, probably favoured by greater humidity and fog present at higher elevations. The positive elevation effect on the richness of rare lichens could be associated with management effect, as the unmanaged forests were located on the highest elevations. Lichen turnover was driven by slope, forest management, and geographical distances. Forest structural features did not play any role in lichen diversity patterns, although management history emerged as an important factor. Unmanaged stands contained many rare species (mostly members of the *Lobarion* community) that we consider indicator species of the absence of forest management in the unmanaged western Pyrenean forests. Surprisingly, *Lobaria pulmonaria*, considered a good indicator of forest management absence, is a widespread species in the western Pyrenees, and its presence is probably linked with high humidity. Hence, it cannot be considered as an indicator of forest management intensity in the studied area.

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KEY WORDS **Forest management; Indicator species; *Lobaria pulmonaria*; Pyrenees; Silver fir–beech forests; Species rarity**

PUBLISHED **Under review in *Ecological Indicators***

ABBREVIATIONS AIC, Akaike Information Criterion; DBH, diameter-at-breast height; GLMM, Generalized Linear Mixed Model; IT, Information-theoretic approach; LAI, Leaf Area Index; MRM, Multiple regression on distance matrices.

1. INTRODUCTION

Beech forests, one of the most transformed European ecosystems, have been thoroughly studied regarding the effects of forest management on biodiversity (Paillet et al., 2010). However, forest management impact on lichen diversity is still scarcely investigated (Johansson, 2008), even though lichens are important components of the biodiversity in European temperate forests (Coppins and Coppins, 2005). It is believed that lichens are valuable bioindicators (Rose, 1992; Nascimbene et al., 2007; Aragón et al., 2010) because they are sensitive to air pollution (Conti and Cecchetti, 2001) and forest habitat quality (Pykälä, 2004; Bergamini et al., 2005). Forest management comprises changes in forest structure and light conditions to which lichens are highly sensitive (Gauslaa and Solhaug, 1996), eventually leading to changes in lichen diversity. Thus, lichen diversity may indicate forest conservation status and be used to evaluate forest management impact.

Lichen richness and composition patterns are regulated by several forest structural and climatic factors (Bartels and Chen, 2012; Nascimbene et al., 2012). Climate operates at the largest scale. For instance, Aragón et al. (2012) found a consistent latitudinal change in lichen species richness and composition along the Mediterranean-temperate transition in Spain because of increased rainfall during the dry season at higher latitudes. At the smallest scale, tree size and age are relevant determinants of epiphyte diversity; larger and older trees maintain more diverse assemblages than younger ones, with many associated species (Fritz et al., 2008; Nascimbene et al., 2009). Tree species are also considered important factors affecting lichen diversity since lichens show affinities for certain physical and chemical rhytidome characteristics (Barkman, 1958; Mežaka et al., 2008). At the stand level, several studies confirmed that lichen communities greatly differ between managed and unmanaged forests in terms of both species richness and composition (Bergamini at al., 2005; Nascimbene et al., 2013b). Unmanaged forests, subject to natural dynamics providing higher structural variation and higher diversity of microhabitats, may host rare species and contain higher species diversity (Friedel et al., 2006). Conversely, in managed forests, old-growth structural features are absent, such as large amounts of dead wood, large living trees, and senescent phases (Commarmot et al., 2005), which can threaten lichen species linked with such habitats (Friedel et al., 2006). As the terms used to describe managed and unmanaged forests across local studies comprise a high variability of management histories, general comparisons are context-sensitive, but it can be generally assumed that the more intensive the management, the larger the difference in plant diversity between managed and unmanaged forests (Horvat et al., 2017a, b; Stephens and Wagner, 2007).

Lichens are generally considered sensitive to environmental changes but, among them, some lichen groups seem to be more affected by forest management. On one hand, cyanolichens are particularly valuable as they are sensitive to forest management and thus confined to old-growth forests (Richardson and Cameron, 2004). On the other hand, several studies focused on rare lichens have reported that they are the most threatened by habitat management (Scheidegger and Goward, 2002) and thus are confined to ancient forest stands (Gustafsson et al., 1999). Lichen life-form is also an important issue to be considered, and some studies have already analysed the sensitivity of specific life-forms to forest management. For instance, it has been reported that crustose lichens are linked with quantity of microhabitats, such as the presence of old trees (Ranius et al., 2008) and that fruticose lichens (e.g., *Alectoria sarmentosa* and *Bryoria* sp.) are highly sensitive to forest practices in boreal forests (Esseen et al., 1996). However, the specific response of each life-form has not yet been addressed in comparative studies.

In recent decades, much attention was dedicated to the foliose lichen *Lobaria pulmonaria* due to its decline in European forests (Barkman, 1958; Rose, 1988; Zoller et al., 1999; Nascimbene et al., 2007). *Lobaria pulmonaria* is generally considered an indicator of old-growth stands (Kuusinen, 1996) and a signal species for assessing forest conservation value (Nascimbene at al., 2007). Its presence is strongly linked with the frequency of rare species (Barkman, 1958; Rose, 1988; Campbell and Fredeen, 2004) which mostly belong to the alliance *Lobarion pulmonariae* Ochsner 1928, a climax community of mature trees (Rose, 1988) with base-rich bark in sheltered habitats (Mucina et al., 2016). The *Lobarion* is best represented in the montane forests of west-central Europe and includes cyanolichens of the genera *Lobaria*, *Nephroma*, *Ricasolia*, *Peltigera*, and some crustose lichens, such as the rare *Thelotrema lepadinum* (Rose, 1988).

Lichens and lichenicolous fungi of the western Pyrenees are well documented, and their diversity is considered one of the highest in Europe (Etayo, 1989, 2010; Etayo and Diederich, 1998). The knowledge acquired by these studies can be used to evaluate management impact, which has still not been studied in Pyrenean forests (Nascimbene et al., 2013b). Traditionally used for animal husbandry and logging, these forests have been managed unsystematically with different logging intensities depending on local population needs. In the western Pyrenees, the information on forest structure is incomplete and has never been researched, in spite of its ecological importance for species diversity. Despite the fact that the Pyrenean landscape has been intensively shaped by grazing and forest management, remote stands have remained relatively well preserved and unmanaged for more than 40 years. These stands could be used as a reference for the research on management effects on lichen diversity.

In this context, the present study addresses the issue of forest management impacts on lichen diversity in the western Pyrenean silver fir–beech forests. According to the literature on this topic, we expected that lichen richness would be higher in unmanaged stands (Dettki and Esseen, 1998; Friedel et al., 2006). We also expected differences in species composition between managed and unmanaged stands (Aude and Poulsen, 2000; Cameron, 2002). Specifically, we aimed to answer the following questions. (1) Which factors drive lichen species richness and turnover? (2) Does forest management affect lichen species diversity? (3) Which lichens indicate management intensity? (4) Is the lichen *Lobaria pulmonaria* an indicator of forest management in this region?

2. MATERIAL AND METHODS

2.1. Study area

The study area is located in the Spanish part of the western Pyrenees, in the regions of Navarre and Aragón (Fig. 1). The landscape is characterised by mountains and valleys with bedrock formed by limestones and marly flysch. Biogeographically, this area belongs to the Alpine Region, and according to the Global Bioclimatic Classification System developed by Rivas-Martínez (2007), the bioclimate is temperate oceanic, with a mean annual temperature of 8°C, mean annual rainfall of 1419 mm, and a W–E continentality gradient. A long history of livestock and forest exploitation shaped the landscape in this area. Consequently, there is large landscape heterogeneity with semi-natural grasslands, scrublands, natural forests, and *Pinus sylvestris* plantations.

The silver fir–beech forests of the area are included in the association *Scillo lilio-hyacinthi–Fagetum sylvaticae* Br.-Bl. ex O. Bolòs 1957, which encompasses ombrophilous, hyperhumid forests growing on calcareous bedrock (Rivas-Martínez et al., 1991). The management history of these stands is unknown because of unsystematically conducted silvicultural practices with different intensities during the last century. Although a high variety of management types were documented (group selection logging, shelterwood, selective logging system, and exclusive fir exploitation), some stands have remained unmanaged for more than 40 years.

2.2. Sampling design

We identified north-facing stands of silver fir–beech forests exceeding 30 ha in an altitudinal range between 800 and 1,700 m above sea level, using potential vegetation maps and aerial photographs provided by the governments of Navarre and Aragón. Twenty stands fulfil these criteria, out of which we chose stands that best represent the categories of managed and unmanaged forests. The selection of managed and unmanaged stands (Appendix A) was based on our previous knowledge about management in this area (Horvat et al., 2017a). As *managed*, we considered recently managed stands (managed from 5 to 20 years ago), whilst as *unmanaged*, we considered the stands in which timber harvesting had not occurred for more than 40 years. We used a nested sampling design in which management was set as a fixed factor with two levels. Within each management level, we chose four stands; within each stand, we randomly sampled four 20 m × 20 m plots, previously used for vegetation surveys. This gave a total of 32 plots in eight clusters (Fig. 1). The rarity of well-preserved forests in the western Pyrenees did not allow us to sample more stands. The presence of lichen species, forest structure, and light regime were recorded in each plot. Field sampling was carried out in 2015 with permits from the governments of Navarre and Aragón.

Presence/absence data of lichens and lichenicolous fungi (hereafter lichens) were recorded. Sampling effort was similar in each plot in terms of time spent censusing and quantity of collected material. All specimens recognised as morphologically different were kept in marked envelopes for further identification in the laboratory. Lichen species nomenclature follows Smith et al. (2009).

Forest structure sampling was based on measuring diameter at breast height (DBH) for all trees within three concentric circles with a radius of 4, 13, and 20 m. In each concentric circle, we recorded all standing trees (living and dead) according to a pre-established DBH threshold

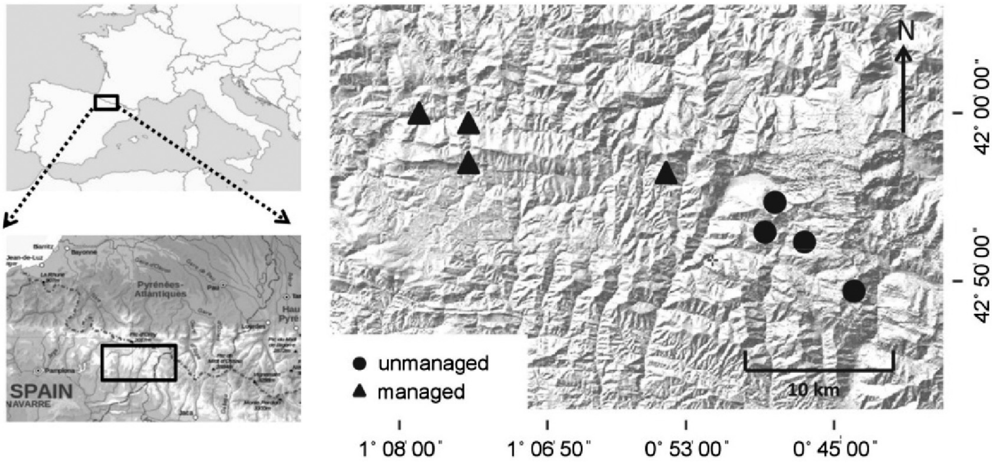

Fig. 1. Study area and location of the eight sampled stands in the western Pyrenees, regions of Navarre, and Aragón, N Spain.

Table 1. Environmental variables used in the analyses of lichen species diversity in western Pyrenean silver fir–beech forests.

Variables	Unit	Managed Mean±SD	Unmanaged Mean±SD
Topography			
Elevation	m a.s.l.	1118 ± 104.70	1447 ± 140.76
Slope	%	46.62 ± 16.21	39.19 ± 12.40
Light conditions			
Transmission	%	10.81 ± 6.13	11.20 ± 2.67
Gaps	%	6.7 ± 5.50	5.9 ± 2.28
Climate			
(T) mean annual temperature	ºC	9.46 ± 0.32	7.95 ± 0.49
(P) annual rainfall (mm)	Mm	1422 ± 73.39	1384 ± 72.33
(Ic) continentality index		15.95 ± 0.42	16.51 ± 0.40
(Io) ombrothermic index		12.63 ± 0.98	14.15 ± 1.10
Forest structure			
Tree density	(N/ha)	638 ± 286	806 ± 617
Number of large trees	(N/ha)	84.29 ± 29.61	88.77 ± 41.85
Number of large fir trees	(N/ha)	39.49 ± 35.20	32.80 ± 41.85
Number of large beech trees	(N/ha)	45.29 ± 31.67	55.97 ± 33.85
Basal area of living trees	(m^2/ha)	34.95 ± 9.41	35.20 ± 12.61
Basal area snags	(m^2/ha)	1.21 ± 2.47	2.27 ± 2.75
Basal area logs	(m^2/ha)	3.89 ± 3.91	2.21 ± 1.80
Total basal area of dead wood	(m^2/ha)	5.09 ± 4.18	4.53 ± 2.77
Number of stumps	(N/plot)	3.68 ± 2.86	2.18 ± 3.63
VarD		50.40 ± 18.23	62.36 ± 17.77

of > 2.5 cm for the 4-m radius circle, > 10 cm for the 13-m radius circle, and > 50 cm for the 20-m radius circle, according to the principle that small trees are measured only on a small area. For deadwood quantification, the diameter of all lying deadwood components (minimum diameter ≥10 cm) was recorded in the 13-m radius circle. To express structural diversity, the coefficient of variation of the diameter distribution (*VarD*) (Sterba and Zingg, 2006) was calculated for each plot. Here, *VarD* is a distance-independent indicator of the vertical structure of a forest stand calculated as follows: *VarD*= 100 × sdDBH/xDBH, where sdDBH is the standard deviation of the DBH classes and xDBH is mean DBH. The living wood volume was not calculated due to the lack of volume tables for this area. The structural variables are specified in Table 1.

Variables of light conditions (Table 1) were obtained by hemispherical photography following VALERI design (Weiss et al., 2001). A detailed protocol of sampling and analysis is described in Horvat et al. (2017a). Considered variables were: *Transmission*, an overall canopy openness or total gap fraction within the defined rings which includes small and large gaps, and *gaps*, the proportion of large gaps which corresponds to between-crown gaps.

Climatic data (Table 1) were derived from digital maps (Ninyerola et al., 2005). Used variables were mean annual temperature (*T*), annual rainfall (*P*), and two bioclimatic indexes (Rivas-Martínez, 2007). The continentality index (*Ic*) is calculated as: *Ic* = Tmax–Tmin, where Tmax is the mean temperature of the warmest month, and Tmin is the mean temperature of the coldest month. The ombrothermic index (*Io*) is given by: $Io = (Pp/Tp) \times 10$, where Pp is the yearly positive precipitation in mm (i.e., total average precipitation of those months with an average temperature higher than 0ºC), and Tp is the yearly positive temperature.

2.3 Data analysis

2.3.1. Species classification and general data exploration

For data analysis, we used several lichen classifications. First, lichens were classified depending on whether the photobiont was a green algae or a cyanobacterium; hence, we distinguished two ecological groups, green algae lichens and cyanolichens. Then, lichens were classified, regarding their life-form, as crustose, fruticose, and foliose lichens. Lastly, species were classified regarding their rarity, which was determined according to the current checklist of the lichens for Spain (Hladun and Llimona, 2002–2007), specific data for the study region (Etayo, 1989, 2010), and expert judgement. We distinguished four levels of rarity for lichen species in the context of beech forests from northern Spain: very common, common, rare, and very rare.

It was not possible to identify all *Usnea* specimens at the species level because of the low quality of collected material and the difficulty of the genus. Hence, for the descriptive analysis (the total number of species), we included all the *Usnea* species identified, which were *Usnea filipendula* agg., *U. florida*, and *U. subfloridana*. However, we used the genus level *Usnea* sp. for the quantitative analysis.

2.3.2. Species richness

We applied generalised linear mixed models to determine the environmental drivers of species richness. As response variables, we used lichen species richness as well as richness of their groups regarding life-form and rarity; the analysis was not performed for groups regarding photobiont type, because of the low number of cyanolichen species (only five). Environmental variables were taken as fixed effects and stand, nested within management, was considered as a random effect. Poisson error distribution for count data and log link function were used. Variables were standardised (zero mean, unit variance), and Spearman correlation analysis was performed to detect collinearity among the environmental variables. Drivers of species richness were analysed using multimodel inference. The full model and all possible sub-models were fitted according to an information-theoretic (IT) approach (Burnham and Anderson, 2002) using the *dredge* function in *MuMIn* package in R. Models were ranked based on their AICc criterion for small sample sizes, which is used as a measure of model quality. The best fitting submodels, models within a distance of 2 AICc units from the first ranking model, were tested for overdispersion. To assess the magnitude of the management effect, we calculated the log response ratio, a suitable metric which expresses proportional differences in species richness between experimental and control stands. Effect sizes of other variables were displayed using the *effects* package in R.

2.3.3. Species composition

We opted for a distance-based variation partitioning approach to quantify the variation explained by each variable and their shared effect on species turnover. This was done both because pairwise dissimilarity indices provide a natural measure for species turnover, and because a distance-based approach allows incorporating the effect of geographical distances into the models, as we were dealing with spatially clustered plots. By variation partitioning, we quantified the contribution of environmental differences and geographical distances to

Table 2. Frequency of rare and very rare lichen species in the managed and unmanaged stands in western Pyrenean silver fir–beech forests. LF, lichenicolous fungi; L, lichen; GA, green algae; C, cyanobacteria; M, managed stands; U, unmanaged stands.

		Rarity	Photobiont type	Life-form	Frequency	
					M	U
L	*Alectoria sarmentosa*	rare	GA	fruticose	0	3
L	*Biatora chrysantha*	rare	GA	crustose	1	1
L	*Biatora vernalis*	rare	GA	crustose	0	2
L	*Bryoria fuscescens*	rare	GA	fruticose	0	2
L	*Buellia erubescens*	rare	GA	crustose	1	0
L	*Catinaria laureri*	rare	GA	crustose	1	0
L	*Evernia illyrica*	rare	GA	fruticose	0	2
LF	*Lichenopuccinia poeltii*	very rare	-	-	0	1
L	*Melanohalea exasperata*	rare	GA	foliose	0	2
L	*Melanohalea exasperatula*	rare	GA	foliose	0	1
L	*Melanohalea laciniatula*	rare	GA	foliose	0	2
L	*Nephroma parile*	rare	C	foliose	0	1
L	*Nephroma resupinatum*	rare	C	foliose	0	3
L	*Parmeliopsis ambigua*	rare	GA	foliose	0	1
L	*Peltigera collina*	rare	C	foliose	0	1
L	*Peltigera degenii*	rare	C	foliose	0	1
L	*Peltigera horizontalis*	rare	C	foliose	1	0
L	*Peltigera hymenina*	rare	C	foliose	1	0
L	*Peltigera praetextata*	rare	C	foliose	1	0
L	*Ricasolia amplissima*	rare	GA	foliose	0	1
L	*Rinodina efflorescens*	very rare	GA	crustose	0	1
LF	*Skyttea tephromelarum*	very rare	-	-	1	0
LF	*Taeniolella phaeophysciae*	rare	-	-	0	1
L	*Thelotrema lepadium*	rare	GA	crustose	1	0
LF	*Tremella hypogymniae*	very rare	-	-	1	0

species turnover, which helps to separate the effects of dispersal limitation and species responses to spatially autocorrelated environmental variables (Tuomisto and Ruokolainen, 2005; Lichstein, 2007). For each explanatory variable, we created the corresponding dissimilarity matrix using Euclidean distance. The matrix of geographical distances was a matrix of linear spatial distances. Firstly, a Mantel test (999 permutations) was run for each dissimilarity matrix to select significant ones. All significant dissimilarity matrices in Mantel tests were included in the Multiple Regression on Distance Matrices analysis (MRM, Lichstein, 2007). After dropping all non-significant variables through backward elimination, the resulting full MRM model was used to quantify the variation explained by each variable, as well as their unique and shared effect. The response variable, total lichen species composition variation was calculated using Sørensen dissimilarity measure. Finally, the differences in species composition were graphically represented by a NMDS (non-metric multidimensional scaling) ordination using Sørensen dissimilarity measure. In each case, we ran 500 NMDS ordinations with random starting configurations to find the most stable solution. The significant variables obtained by MRM were passively projected on the ordination graph. Multivariate analyses were performed with *vegan* and *ecodist* packages in R.

Table 3. Lichen diversity measures in managed and unmanaged stands in silver fir–beech forests from the western Pyrenees.

	Managed Mean±SD	**Unmanaged Mean±SD**
Total lichen richness	8.96 ± 4.12	10.50 ± 4.13
Crustose lichen richness	2.93 ± 2.37	1.62 ± 1.36
Foliose lichen richness	4.25 ± 1.80	5.56 ± 2.25
Fruticose lichen richness	1.68 ± 0.87	2.68 ± 1.07
Green algae lichen richness	8.81 ± 3.91	9.56 ± 3.59
Cyanobacterial lichen richness	0.18 ± 0.40	0.37 ± 0.61
Richness of very common lichens	4.93 ± 1.73	4.18 ± 1.51
Richness of common lichens	3.18 ± 2.45	4.25 ± 1.94
Richness of rare lichens	0.56 ± 0.72	1.50 ± 1.15
Richness of very rare lichens	0.12 ± 0.34	0.06 ± 0.25

Additionally, we conducted an indicator species analysis using the IndVal index (Dufrêne and Legendre, 1997) to assess the affinity of lichen species for the management categories. All analyses were run using (v. 3.2-5) R statistical environment (R Foundation for Statistical Computing, Vienna, AT), except indicator species analysis, which was performed using the Ginkgo program (De Cáceres et al., 2007).

3. RESULTS

3.1. Overall floristic results

In the overall survey of 32 plots, we identified 66 lichens (including four lichenicolous fungi). We recorded 40 species in managed stands and 45 in unmanaged ones. The mean total richness per plot was 9.40 ± 3.85. Thirty species (45% of total species) occurred only in one single plot. The most frequent lichen species were: *Parmelia saxatilis* (in 81% of the plots), *Pseudevernia furfuracea* (78%), *Parmelia sulcata* (68%), and *Lobaria pulmonaria* (65%). Lichen richness was quite balanced among life-form types, with 39% crustose, 39% foliose, and 22% fruticose lichens. Regarding photobiont type, 11% were cyanolichens. Only 6% were very rare species, 35% were rare, and 59% were common or very common (Appendix B). Rare and very rare species were recorded in both managed and unmanaged stands (Table 2). Total lichen richness was similar in managed and unmanaged stands, but unmanaged stands contained on average almost three times more rare lichens (Table 3).

3.2. Environmental variability

The tree layer was dominated by beech (*Fagus sylvatica* L.), followed by silver fir (*Abies alba* Mill.). *Transmission*, overall canopy openness, and *gaps*, percentage of large gaps, were highly correlated ($r = 0.92$). *Transmission* average was 11.1%, whilst the *gaps* average was 6.3%; thus, the percentage of large gaps described more than half of overall canopy openness. The highest mean value for the *gaps* variable was found in the managed stand San Fermín, with gaps created by management practices, and in the unmanaged stand Aztaparreta, where gaps were created by natural disturbances.

Climatic conditions differed over the sampled area because of the 40-km long transect in an E–W direction (Table 1). Managed stands were located in the western part of study area, which

Table 4. Summary results of GLMMs explaining the total lichen species richness and richness of their groups with respect to predictor variables. Poisson error distribution for count data and log link function were used. Stand was included as a random factor, nested within the management category. * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

Lichen species richness ~ slope + (1 | stand)				
	Estimate	**Std. error**	**Z value**	**Pr (>|z|)**
(intercept)	2.221	0.115	19.181	<2e-16***
Slope	-0.1759	0.08	-2.199	0.0279*

Fruticose lichen richness ~ elevation + (1 | stand)				
	Estimate	**Std. error**	**Z value**	**Pr (>|z|)**
(intercept)	0.7471	0.1237	6.039	1.55e-09***
Elevation	0.2694	0.1203	2.240	0.0251*

Rare lichen richness ~ elevation + (1 | stand)				
	Estimate	**Std. error**	**Z value**	**Pr (>|z|)**
(intercept)	-0.1389	0.2029	-0.685	0.49349
Elevation	0.5886	0.1827	3.222	0.00127**

Table 5. Results of the multiple regression on distance matrices analysis (MRM) for total lichen species turnover in silver fir–beech stands from the western Pyrenees showing the unique and shared effects of significant variables. Significant environmental variables were slope and management type.

Response: lichen species composition	Variation explained (%)
turnover~space+slope+management (full model)	12.18
turnover~space	5.8
turnover~slope	4.6
turnover~management	2.3
turnover~slope + management	6.6
space unique effect	6.2
environmental unique effect	7
shared effect	-0.4
slope unique effect	3.1
management unique effect	4

corresponds to lower elevations with higher mean annual temperature. Conversely, unmanaged stands were concentrated in the eastern part, at higher elevations, and showed higher continentality and ombrothermic indices (Table 1).

Regarding forest structural features, managed and unmanaged stands had similar forest structure, although unmanaged forests showed a tendency to have less stumps, a higher density of small trees, and an increased basal area in larger DBH classes (unpublished results).

3.3 Drivers of species richness

The GLMM showed that lichen species richness is negatively affected by slope (Table 4), but the effect of this variable was weak (Fig. 2a). Crustose and foliose lichen richness did not respond to any variable, whilst fruticose and rare lichen richness responded positively to elevation with a moderate effect (Table 4, Fig. 2b,c).

3.4. Species turnover

The multiple regression on distance matrices analysis explained 12.2% of total lichen turnover with three variables: geographical distance, slope, and management type (Table 5, Fig. 3). Environmental fraction and geographical distances explained a similar level of variation, 7% and 6.2%, respectively. The shared effect between space and environmental variables returned a negative value; however, this was small. Unique contributions of the two environmental factors ranged from 3.0% to 4.0%.

The NMDS ordination showed that managed and unmanaged plots are slightly clustered (Fig. 3).

3.5. Indicator species analysis

The indicator species analysis for management categories showed that the only significant species ($p < 0.05$) were *Lecanora argentata*, diagnostic for the managed stands (IndVal = 0.612), and *Melanelixia fuliginosa* subsp. *glabratula*, for unmanaged stands (IndVal = 0.763).

4. DISCUSSION

4.1. General patterns

This study provides insights into lichen species diversity in silver fir–beech forests from the western Pyrenees in relation to relevant environmental variables as well as their indicator values according to management type.

Mean lichen richness of unmanaged Pyrenean forests (10.5 species in 400 m^2) was similar to Carpathian primeval beech forests, where the mean richness was 10.2 species in plots of 500

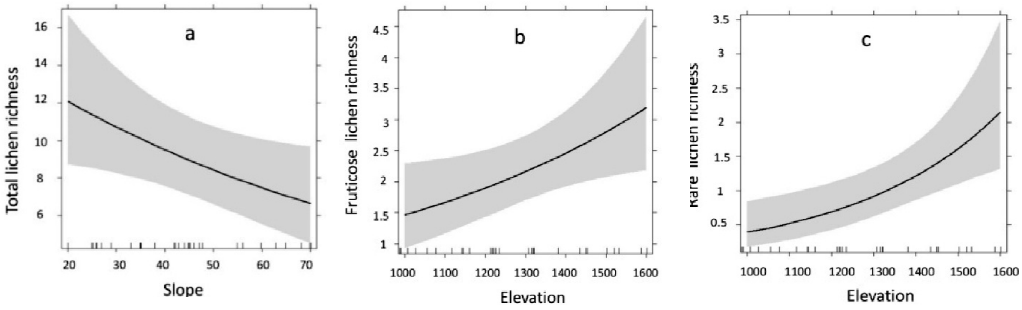

Fig. 2. (a) Model response of total lichen richness to slope as predicted by GLMMs, with 95% confidence intervals. Vertical axis is displayed on the scale of the response. The effect of slope on lichen richness was weak; for a slope increase of 20% (from 20 to 24%) lichen richness decreased approximately 5% (from 12.1 to 11.5). (b) Model response of fruticose lichen richness to elevation as predicted by GLMMs with 95% confidence intervals. The effect of elevation on fruticose lichen richness was weak; for an elevation increase of 20% (from 1000 to 1200), fruticose lichen richness increased 23% (from 1.5 to 1.9). (c) Model response of rare lichen richness to elevation as predicted by GLMMs with 95% confidence intervals. Effect of elevation on rare lichen richness was moderate; for an elevation increase of 20% (from 1000 to 1200), rare lichen richness increased 43% (from 0.4 to 0.7).

m^2 (Dymytrova et al., 2014). With a mean species richness of 9.0 species per plot, managed Pyrenean forests can also be considered species-rich. Floristic studies on Pyrenean lichens reported that these forests are a hotspot of lichen diversity due to their favourable climatic conditions and good conservation conditions (Etayo, 1989, 2010).

The high number of rare and very rare species confirms that western Pyrenean forests are suitable habitats for high lichen richness (Martínez et al., 2006). Although rare species have been mostly recorded in the unmanaged stands, some of them have been recorded only in the managed ones. It is worth mentioning that the rare lichens *Buellia erubescens*, *Catinaria laureri*, *Peltigera horizontalis*, *P. hymenina*, *P. praetextata*, and *Thelotrema lepadinum*, found only in the managed Pyrenean stands, have been reported as indicators of well-preserved forests (Selva, 1996; Motiejknait et al., 2004; Smith et al., 2009; Hofmeister et al., 2016). Their presence in the managed Pyrenean forests may be explained either by the relatively good conservation conditions of these forests, including managed ones, or by the favourable climatic conditions prevailing in this area (Etayo, 1989, 2010). The four very rare species were evenly distributed in managed and unmanaged stands. Among them, the crustose *Rinodina efflorescens* was only present in the old-growth forest Aztaparreta. We must mention, anyway, that its ecological affinities are not well known, as it has been scarcely recorded in Europe and North America (Purvis et al., 1992). Other very rare species were the lichenicolous fungi *Lichenopuccinia poeltii*, recorded in an unmanaged forest, and *Skyttea tephromelarum* and *Tremella hypogymniae*, both recorded in managed forests. Although the ecology and distribution of lichenicolous fungi is still limited (Gams et al., 2004), they should receive more attention as potential indicators of old-growth forests.

4.2. Species richness

According to our results, slope is the most important driver of total lichen species richness in western Pyrenean silver fir-beech forests. Slope ranged from 10 to 76% in the sampled plots, and lichen richness decreased at steeper slopes, where lichens are exposed to higher light le-

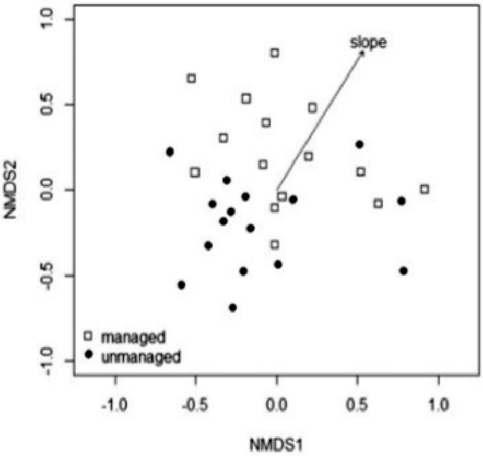

Fig. 3. Non-Metric Multidimensional (NMDS) ordination based on compositional data of all lichen species in 32 plots in the silver fir–beech forests from the western Pyrenees. Lichen species composition variation was based on Sørensen dissimilarity measure, and the final three-dimensional solution was reached after 20 iterations with a final stress of 0.15. Symbols represent plots according to their management type. Vectors represent environmental variables detected by MRM analysis.

vels and to consequent drought which have a great negative influence on lichens (Heylen et al., 2005; Werth et al., 2005). The steep slopes are also exposed to higher wind speeds, due to lower tree density, which could potentially increase lichen desiccation (Anstett and Coiner, 2010). Forest management did not have any effect on total lichen richness in western Pyrenean forests, although several studies have reported significant differences in species richness between managed and unmanaged forests (Dettki and Esseen, 1998; Friedel et al., 2006).

The increase of fruticose lichen richness with elevation might be interpreted as the positive effect of higher air humidity on this lichen group. As the fruticose lichens are aero-hygrophytic species (Nascimbene et al., 2007), the fog and high humidity at the highest elevations favour their occurrence, as already observed by Rose (1988).

The richness of rare species was also best explained by elevational gradient, although the management type was a significant variable when entered separately in the model. As elevation was spatially correlated with management type (i.e., unmanaged stands were located at the highest elevations), we cannot disentangle the effects of these two variables. Both elevation and management might affect the richness of rare species. On one hand, the hypothetical management effect could be supported by the fact that most rare species recorded exclusively in the unmanaged Pyrenean stands are described in the literature as indicators of ancient forests (Rose, 1992; Esseen et al., 1996; Esseen, 2006; Smith et al., 2009; Nascimbene et al., 2013b). On the other hand, some of these rare species, especially the fruticose ones (*Alectoria sarmentosa*, *Bryoria fuscescens*, and *Evernia illyrica*) have an affinity for high elevations and humidity (Rose, 1988); hence, they might occur at the highest elevations in unmanaged forests because of their ecological requirement for higher humidity, not strictly due to management absence. Similar conclusions were drawn in Italy, where many rare species at the national level are mainly occurring in sites with high humidity (Nimis and Martellos, 2017).

4.3. Species turnover

In the western Pyrenean forests, the predictors of lichen species turnover retained by multiple regression were related with space and environmental heterogeneity. The largest part of variation explained by geographical distance suggests the existence of dispersal limitation or the possibility that some variables remained unmeasured. Previous studies on this topic have reported dispersal limitation for many epiphytic lichens (e.g., *Bryoria* sp., *Lobaria pulmonaria*, and *Nephroma parile*), which reproduce by vegetative propagules and, as such, their dispersal is limited to shorter distances than the dispersal of lichens reproducing by sexual spores (Scheidegger et al., 1998). Consequently, these species have low colonisation rates and seem to be restricted to old-growth stands rather than to young ones (Sillett et al., 2000; Dettki et al., 2016). Regarding unmeasured variables, they might be related, on the one hand, to variables of microhabitats, which are difficult to control (e.g., thickness and irregularity of the rhytidome). On the other hand, several studies have reported that lichens are sensitive to air pollution (Hawksworth and Rose, 1976), but we excluded this factor because the forests in the studied area are far from road traffic and have low pollution levels.

The negative shared effect between environmental factors and geographical distance may indicate correlation between the variables, a common problem in variance partitioning techniques (Sabatini et al., 2014). Management type explained a small part of the variation in lichen turnover, but forest structural features did not have any effect, contrary to that observed in other studies (Friedel et al., 2006). Actually, current forest structural features might mask the effect of management history (Gossner et al., 2014). In this case, the effect of management might be explained by the different management histories of managed and unmanaged forests, including time since last logging and forest continuity, which are important factors for lichen diversity (Fritz et al., 2008; Marmor et al. 2011; Nascimbene et al., 2013b). Our results of management effect on lichen species composition are consistent with several studies carried out in different European forest types: Mediterranean oak forests (Aragón et al., 2010), boreal spruce forests (Esseen et al., 1996), and temperate deciduous forests (Nascimbene et al., 2013a; Dymytrova et al., 2018).

Slope also contributed to total lichen species turnover because of species preference for certain ecological requirements. Pioneer lichen species, such as *Alectoria sarmentosa*, *Cladonia pyxidiata*, and *Pertusaria albescens*, with preference for light exposure and wind, occur more frequently on the steepest slopes, whilst *Cladonia fimbriata*, *Nephroma resupinatum*, and *Usnea* sp. are more frequent on gentle slopes.

4.4. Indicator species analysis

Indicator species analysis revealed only two diagnostic species: *Lecanora argentata* for the managed Pyrenean silver fir-beech forests and *Melanelixia fuliginosa* subsp. *glabratula* for the unmanaged ones. *Lecanora argentata* is reported as a common species in European beech forests (Nimis and Martellos, 2017). According to our own observations in the studied region, *L. argentata* colonises exposed smooth cortex of beech trees, but disappears when the cortex is covered by mosses and other lichens (e.g., *Parmeliaceae*); hence, it can be considered an indicator of frequent disturbances by thinning. According to Nimis (2016), *M. fuliginosa* subsp. *glabratula* is a common ecologically wide-ranging species that grows on several phorophytes (especially *Quercus* and *Fagus*) and also occurs in managed open forests. Nevertheless, we suggest that its indicator value for Pyrenean unmanaged forests should be further investigated.

According to our results, many rare lichens occur only in unmanaged forests, but they are not recognised as indicator species by the indicator species analysis due to their low frequency, as IndVal is a symmetric index that gives a higher weight to the common species (Dufrêne and Legendre, 1997). However, many of them have been reported as indicators of ancient forests in other regions, such as *Nephroma parile*, *N. resupinatum*, *Peltigera collina*, *P. degeni*, and *Ricasolia amplissima*, which are diagnostic species from the *Lobarion* community (Rose, 1988). Besides, some of these species are considered threatened lichens in Spain (Martínez et al., 2006). Thus, we support the previous observations and confirm that these species from the *Lobarion* community are suitable indicator species for Pyrenean unmanaged forests.

Other rare species recorded only in the unmanaged forests have been scarcely studied, and little information is available. More knowledge is needed to confirm their indicator value in the context of their sensitivity for forest management. For instance, the fruticose *Evernia illyrica* is a montane species dependent on high humidity (Nimis, 2016), but we could also consider it an indicator species for unmanaged forests as it is included on the Italian red list as extremely rare and endangered (Nascimbene et al., 2013) and it has been recorded in an old-growth forest in northern Spain (Barreno and Pérez-Ortega, 2003a). Furthermore, in the Pyrenees, it has only been reported growing on large trees in well-preserved forests (Etayo, 2010). *Alectoria sarmentosa* and *Bryoria fuscescens* have both been reported as sensitive to forest management in boreal forests (Esseen et al., 1996; Esseen, 2006). In southern Europe, however, they are considered as common species at the highest elevations (Rose, 1988), which is consistent with our results about their higher frequency. *Biatora vernalis* has been mentioned in the literature as an indicator of well-preserved forests (Smith et al., 2009; Dymytrova et al., 2014), but its distribution is still poorly known (Printzen and Palice, 1999) and more research is needed to evaluate its potential use as an indicator species. Although rare in Pyrenean forests, *Melanohalea* *exasperata* is a common species in the sub-Mediterranean belt in Spain. A similar pattern is observed in Italy for *M. exasperatula*, which is common in the Alps (Nimis, 2016). Hence, its rarity in Pyrenean forests is probably due to its ecological requirements for a warmer climate, not the management effect. The indicator value of *Melanohalea laciniatula*, a montane species growing on the bark of old beech trees in humid forests (Nimis, 2016), for unmanaged forests should be taken into account and further analysed by means of a larger data set based on more extensive sampling.

In summary, our study is able to provide only limited insight into the sensitivity of rare lichens to forest management due to the little knowledge on their distribution and to the small size of our dataset. Hence, the management impact could not be clearly disentangled from rarity, as rarity might be also caused by a combination of environmental- and dispersal-related factors. *Lobaria pulmonaria*, generally considered the best indicator for unmanaged forests (Nascimbene et al., 2007), is a widespread species in the western Pyrenees, where it grows in many forests, regardless of their management type. Hence, it cannot be considered a good indicator species for unmanaged stands in the western Pyrenees. Its presence is probably linked with high air humidity and fog in this region.

5. CONCLUSIONS

After analyzing different aspects of lichen diversity in western Pyrenean silver fir–beech forests, our main conclusion is that lichen richness mainly depends on topographic and climatic factors, whilst forest management affects species composition. As regards to the foliose lichen *Lobaria pulmonaria*, frequently considered an indicator species of unmanaged forests, we suggest that its presence in western Pyrenean forests is an indicator of climatic factors, mainly air humidity, rather than forest management. Rare lichens are relatively more frequent in the unmanaged forests, but we can only extract partial conclusions about their indicator value for Pyrenean forests. Our recommendations for forest managers include avoiding clear-cuts and applying selective tree logging to preserve large foliose lichens from the *Lobarion* community, which are mostly sciophilous species. Our study contributes to understanding lichen diversity patterns, especially when many questions are still open, such as the influence of management types and management history. As the forest management in the western Pyrenees is an intricate issue, our study just reaches to confirm differences in species composition between managed forests and those without forest management for 40 years. Developing knowledge on indicator species in this region deserves special attention.

ACKNOWLEDGEMENTS

We thank Jorge García de Vicuña, Almudena Pereda Romero and Raul Ilundain for help in field sampling.

Funds from the project IT299-10 for research groups of the Basque Government have been used for this survey.

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SUPPLEMENTARY MATERIAL

APPENDIX A. Characteristics of the sampled stands in the study on lichen diversity in western Pyrenean silver fir-beech forests.

	Management category	Elevation (m a.s.l.)	Stand's coordinates (x,y)	Stand surface area (ha)
Lizardoia	managed	980-1080	0653820, 4763330	49
San Fermin	managed	1000-1230	0655930, 4761810	49
Eskalera	managed	990-1140	0654482, 4760315	30
Pikatua	managed	1110-1300	0661514, 4758615	32
Maze	unmanaged	1320-1520	0677288, 4751014	68
Aztaparreta	unmanaged	1600-1650	0677940, 4753194	93
Gamueta	unmanaged	1340-1530	0679985, 4750580	82
Selva de Oza	unmanaged	1200-1400	0686280, 4744519	32

APPENDIX B. Lichen species found in western Pyrenean silver fir-beech forests with indication of their photobiont type, life-form and rarity and their frequency. L, lichen; LF, lichenicolous fungi; GA, green algae; CY, cyanobacteria; VC, very common species; C, common species; R, rare species; VR, very rare species.

	Species	Photobiont type	Life-form	Rarity	Frequency
L	*Alectoria sarmentosa*	GA	fruticose	R	3
L	*Biatora chrysantha*	GA	crustose	R	2
L	*Biatora vernalis*	GA	crustose	R	2
L	*Bryoria fuscescens*	GA	fruticose	R	2
L	*Buellia erubescens*	GA	crustose	R	1
L	*Buellia griseovirens*	GA	crustose	C	2
L	*Catinaria laureri*	GA	crustose	R	1
L	*Cladonia coniocraea*	GA	fruticose	VC	1
L	*Cladonia fimbriata*	GA	fruticose	VC	3
L	*Cladonia macilenta*	GA	fruticose	C	1
L	*Cladonia pyxidata*	GA	fruticose	C	3
L	*Evernia illyrica*	GA	fruticose	R	2
L	*Evernia prunastri*	GA	fruticose	VC	7
L	*Fuscidea cyathoides*	GA	crustose	C	1
L	*Hypogymnia physodes*	GA	foliose	VC	20
L	*Hypogymnia tubulosa*	GA	foliose	C	11
L	*Lecanora argentata*	GA	crustose	VC	6
L	*Lecanora carpinea*	GA	crustose	C	1
L	*Lecanora chlarotera*	GA	crustose	C	1
L	*Lecanora intumescens*	GA	crustose	C	5
L	*Lecidella elaechroma*	GA	crustose	C	1
L	*Lepraria lobificans*	GA	crustose	C	1
L	*Lepraria* sp.	GA	crustose	-	6
LF	*Lichenopuccinia poeltii*	-	-	VR	1
L	*Lobaria pulmonaria*	GA	foliose	C	21
L	*Melanelixia* sp.	GA	foliose	-	13
L	*Melanelixia fuliginosa* subsp. *glabratula*	GA	foliose	C	1
L	*Melanelixia subaurifera*	GA	foliose	C	1
L	*Melanohalea exasperata*	GA	foliose	R	2
L	*Melanohalea exasperatula*	GA	foliose	R	1
L	*Melanohalea laciniatula*	GA	foliose	R	2
L	*Mycobilimbia pilularis*	GA	crustose	C	1
L	*Nephroma parile*	CY	foliose	R	1
L	*Nephroma resupinatum*	CY	foliose	R	3
L	*Opegrapha rufescens*	GA	crustose	C	1
L	*Parmelia saxatilis*	GA	foliose	VC	26
L	*Parmelia sulcata*	GA	foliose	VC	22
L	*Parmelina pastillifera*	GA	foliose	C	3
L	*Parmeliopsis ambigua*	GA	foliose	R	1
L	*Peltigera collina*	CY	foliose	R	1
L	*Peltigera degenii*	CY	foliose	R	1
L	*Peltigera horizonatlis*	CY	foliose	R	1
L	*Peltigera hymenina*	CY	foliose	R	1
L	*Peltigera praetextata*	CY	foliose	R	1

APPENDIX B. (Cont.).

	Species	Photobiont type	Life-form	Rarity	Frequency
L	*Pertusaria albescens*	GA	crustose	VC	10
L	*Pertusaria amara*	GA	crustose	C	11
L	*Pertusaria flavida*	GA	crustose	C	2
L	*Pertusaria pertusa*	GA	crustose	C	3
L	*Phlyctis argena*	GA	crustose	VC	11
L	*Physcia tenella*	GA	foliose	C	1
L	*Physconia distorta*	GA	foliose	C	2
L	*Platismatia glauca*	GA	foliose	C	17
L	*Pseudevernia furfuracea*	GA	fruticose	VC	25
L	*Pyrenula nitida*	GA	crustose	C	1
L	*Pyrenula* sp.	GA	crustose	-	1
L	*Ramalina farinacea*	GA	fruticose	VC	15
L	*Ramalina fastigiata*	GA	fruticose	C	4
L	*Ricasolia amplissima*	GA	foliose	R	1
L	*Rinodina efflorescens*	GA	crustose	VR	1
LF	*Skyttea tephromelarum*	-	-	VR	1
LF	*Taeniolella phaeophysciae*	-	-	R	1
L	*Thelotrema lepadinum*	GA	crustose	R	1
LF	*Tremella hypogymniae*	-	-	VR	1
L	*Usnea filipendula* agg.	GA	fruticose	C	1
L	*Usnea florida*	GA	fruticose	R	2
L	*Usnea subfloridana*	GA	fruticose	C	1

Vlatka Horvat (2018) PhD THESIS pp. 147-149

7. Overview of results and summary of conclusions

This dissertation contributes to knowledge about the effect of management on the structure of forests and the diversity of vascular plants, bryophytes, and lichens in the silver fir-beech forests of the western Pyrenees. The main finding is that forest management affected all three taxonomic groups in terms of species richness or species composition, despite the difficulties in defining the type, intensity, and frequency of silvicultural management.

In the first study, where the impact of forest management on vascular plant diversity was analysed, categorization of management was based on the time elapsed since the cessation of management, although the intensity of management was also taken into account. Four management categories were therefore established: 'recently-managed', 'long-managed', 'recently-abandoned', and 'long-abandoned'. The results showed that past management is one of the most important factors affecting present vascular plants species diversity. In particular, the species richness of vascular plants decreased in the 'recently-abandoned' stands, corresponding to a period of abandonment of approximately 40 years. Herb-layer composition also varied across the management types. In addition, the large forest gaps, which may be a consequence of either management practices or natural disturbances, positively affected the species richness of vascular plants with a niche preference for open areas. My results stressed that both the time since cessation of management and the management history are important for the recovery of the herb-layer diversity. Nevertheless, environmental factors, such as slope and climate, also play a role in shaping herb-layer patterns.

My subsequent research on impact of forest management was focused on bryophytes, which are considered more sensitive to management practices than vascular plants. In this case, management categorization was focused on the intensity of management, which is correlated, to some extent, with the time elapsed since cessation of management. Three categories were established: 'intensive', 'moderate', and 'low' management intensities. The results showed that the total bryophyte species richness decreases with intensive forest management, which comprises logging of large trees and stand homogenization. This causes the loss of microhabitats and, consequently, decreases bryophyte diversity. Moderate management intensity, which integrates sustainable forest management, preservation of large trees and preservation of sufficient dead wood, did not affect bryophyte diversity. Apart from forest management, bryophyte species richness was also influenced by elevation above mean sea level, corresponding to a shift in climatic conditions, a factor already shown to be an important driver of bryophyte diversity.

In the first two studies dealing with vascular plants and bryophytes, forest management was based either on the time elapsed since silvicultural interventions or on the intensity of management, and I concluded that both aspects of management affect plant diversity. To quantify the differences in structural features between managed and unmanaged forests, I selected a subset of the previously used data, in which unmanaged stands and long-abandoned stands were included under the 'unmanaged' category, whilst the 'managed' category included stands that are currently managed. Both managed and unmanaged stands showed similar structural features of forest regarding basal area, tree density, structural heterogeneity, and light conditions. These results may indicate that the currently applied management practice in the forests of the western Pyrenees is relatively sustainable. Interestingly, managed forests had higher densities of silver fir than unmanaged ones, this probably being a consequence of past management practices favouring this species. Additionally, a shift in the distribution of the basal area of unmanaged stands towards larger diameter classes was also observed. Although the abandonment of forest management is relatively recent, it appears that unmanaged stands are recovering old-growth attributes after decades of exploitation, and may be considered well-preserved forests in the European context. Therefore, these unmanaged forests could be used as reference stands in studies on the effects of management on plant diversity in the western Pyrenees.

The same subset of data, along with data on forest structure and soil properties, was used for a comparative study of the effect of forest management on vascular plants and bryophytes. The results showed that elevation is driving the species richness of both vascular plants and bryophytes. However, our data set clustered managed and unmanaged stands in blocks of low and high elevations, and the effect of elevation may therefore have been confounded with the effect of management. Vascular plants and bryophytes responded differently to the other environmental variables. The species richness of vascular plants was driven by silt content and large gaps, whilst their turnover was influenced by aluminium saturation which was highly correlated with soil pH. Conversely, bryophyte diversity was not clearly affected by any of the measured environmental variables. Hence, I suggest that vascular plants and bryophytes should be investigated separately in studies of the impact of forest management on plant diversity.

The response of lichens to forest management was also assessed using the same subset of data. According to my results, richness of lichens is not affected by forest practices in the western Pyrenean forests, but, their turnover does respond to forest management. This management effect might be due to different management histories of managed and unmanaged stands, as forest structural features did not affect lichen turnover. Additionally, both the richness of lichens and their turnover were driven by slope. Lichen richness decreases on steep slopes, probably because of increased lichen desiccation. We also conducted an Indicator Species Analysis, according to which *Lecanora argentata* could be considered an indicator species for the managed Pyrenean silver fir-beech forests. On the other hand, species from the *Lobarion* community may be considered indicators of unmanaged Pyrenean forests. However, *Lobaria pulmonaria* itself is a widespread species in this region, and this reduces its usefulness as an indicator species in the western Pyrenees.

The results of this thesis could serve for informing and improving future forest management strategies that focus on conservation of biodiversity. As regards general recommendations for sustainable management, I advocate that current forest management is adequate for preserving biodiversity, but I also suggest that any kind of intensive forest cover removal should be avoided in the Pyrenean silver fir-beech forests, since intensive forest management affects bryophyte diversity negatively. Furthermore, stand homogenization should be avoided, and the target logging of large trees minimized in order to preserve important microhabitats for bryophyte and lichen diversity. For the same reasons, sufficient quantities of laying and standing dead wood should be retained after logging. My results stressed that slope plays an important role in species diversity of all three taxonomic groups, so another recommendation is that tree logging in such steep slopes, which are prone to erosion, should be reduced in frequency and intensity, or discontinued altogether.

SUMMARY OF CONCLUSIONS

1. Vascular plants and bryophytes should be analysed separately in studies assessing the impact of management on forests, as they present different patterns of diversity in the studied forests
2. Recent abandonment of forest management in the western Pyrenean silver fir-beech forests decreases the richness of vascular plants adapted to high light levels, whilst intensive forest management is the principal factor leading to the loss of bryophyte species
3. Forest management history of the Pyrenean silver fir-beech forest affects lichen species composition. The rare lichens from the *Lobarion pulmonariae* community are the most affected. I suggest the use of these species as good indicators of unmanaged Pyrenean forests
4. The effect of forest management on plant diversity maybe confounded with the effect of elevation, since most of the unmanaged forests are located at the highest elevations. This interaction is complicating the interpretation of the results, but it is a factor inherent to the studied forests and cannot be discounted
5. In the Pyrenean silver fir-beech forests, structural features do not have a major effect on plant species diversity, but management history does exert a significant influence
6. Unmanaged Pyrenean forests still do not show old-growth attributes, as these stands are in the ongoing process to reach the terminal phase. However managed stands may be considered to be well-preserved due to their structural complexity