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

Vlatka Horvat[a], Patxi Heras[b], Itziar García-Mijangos[a,*], Idoia Biurrun[a]

[a] Dept. Plant Biology and Ecology, Faculty of Science and Technology, University of the Basque Country, P.O. Box 644, 48080 Bilbao, Spain
[b] Siervas de Jesús 24, 01001 Vitoria, Spain

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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.

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 (Kantvilas et al., 2015; Nelson and Halpern, 2005). 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, 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 (Bengtsson et al., 2000; Paillet et al., 2010; Peterken, 1996). Forest structure determines the light conditions, which

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

* Corresponding author.
E-mail addresses: vhorvat001@ikasle.ehu.es (V. Horvat), bazzania@arrakis.es (P. Heras), itziar.garcia@ehu.es (I. García-Mijangos), idoia.biurrun@ehu.es (I. Biurrun).

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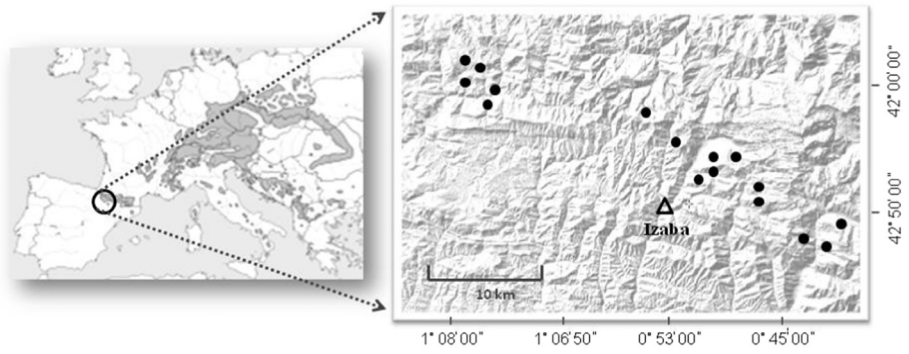

Fig. 1. *Abies alba* distribution (EUFORGEN, 2009, www.euforgen.org, last accessed 20.5.2016) and location of the 16 sampled stands in the western Pyrenees, regions of Navarre and Aragon, northern Spain.

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 (Jonsson et al., 2015; Mills et al., 2004; Vellak and Ingerpuu, 2005), whilst this knowledge is scarcer in European temperate forests (Müller et al., 2015; Bardat and Aubert, 2007; Király and Ódor, 2010). 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 (Friedel et al., 2006; Vellak and Ingerpuu, 2005), 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 (Fenton and Frego, 2005; Lesica et al., 1991). 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 Aragon (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 Aragon. 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.