

## **A comparison between the diaspore bank and above-ground bryoflora in the beech forests of Navarra (Northern Spain)**

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**Abstract** – Bryophyte diaspore banks remain poorly known, especially those from Atlantic forests. Here we describe the composition and characteristics of diaspore banks in Atlantic beech forests (*Fagus sylvatica*) (Navarra, Northern Spain) and compare them with above-ground vegetation. Soil samples from nine beech forests were cultivated for eight-nine months and germinating species were identified; we also collected above-ground bryophytes in the same beech forests. The diaspore bank has 40 species, and there is strong positive correlation between the floristic richness in the diaspore bank and in the corresponding above-ground vegetation. The specific composition of the two ecological compartments is very different; only *Fissidens taxifolius* and *Polytrichum formosum* are always frequent. Some species in diaspore bank are very uncommon in above-ground vegetation (*Pohlia andalusica*, *Trichodon cylindricus*); we postulate that some species are dispersed over a long distance. Colonist species are the most frequent in the diaspore bank, while perennials dominate in above-ground vegetation. This contrast is reduced in acidophytic beech forests, mainly due to the high number of colonist liverworts in the above-ground vegetation.

**Mosses / liverworts / Atlantic forests / *Fagus sylvatica* / *Quercus-Fagetea* / biodiversity / floristic richness / life strategies / long-distance dispersal**

**Résumé** – Les banques de diaspores de bryophytes restent peu connues, notamment celles des forêts atlantiques. Ici, les auteurs décrivent la composition et les caractéristiques des banques de diaspores des hêtraies atlantiques (*Fagus sylvatica*) (Navarre, Espagne N) et les comparent à la végétation du sol. Les échantillons de sols de 9 forêts de hêtraies ont été cultivés pendant 89 mois et les espèces qui ont germées ont été identifiées ; les bryophytes au-dessus du sol ont été récoltés dans ces mêmes forêts. La banque de diaspores contient 40 espèces, et il y a une très forte corrélation positive entre la richesse floristique dans la banque diaspore et la végétation correspondante au-dessus du sol. La composition spécifique des deux compartiments écologiques est très différente : seuls *Fissidens taxifolius* et *Polytrichum formosum* sont toujours fréquents. Quelques espèces de la banque de diaspore sont très rares dans la végétation above ground (*Pohlia andalusica*, *Trichodon cylindricus*) ; il est postulé que quelques espèces sont dispersées sur une longue distance. Les espèces colonistes sont les plus fréquentes dans la banque de diaspores, tandis que les pérennes dominent la végétation au dessus du sol. Ce contraste est réduit dans les hêtraies acidophytiques, principalement à cause du grand nombre d'hépatiques colonistes dans la végétation above-ground.

**Mousses / hépatiques / forêts Atlantiques forests / *Fagus sylvatica* / *Quercus-Fagetea* / biodiversité / richesse floristique / strategies de vie / dispersion longue distance**

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## INTRODUCTION

The term “diaspore” is used for any structure, organ or fragment of a plant which is capable of regenerating a new individual whenever environmental conditions are suitable (During, 1997; Ross-Davis & Frego, 2004; Piudo & Caverio, 2005; Hock *et al.*, 2006). Viable seeds and fruits are diaspores of vascular plants and spores, tubers, bulbils, rhizoidal gemmae, or specialized caducous organs are well known as bryophyte diaspores (During, 1997; Thompson *et al.*, 1997; Frey & Kürschner, 2011). The diaspores may not germinate immediately when they fall on the soil, since they may remain there for a time, constituting the so-called “soil diaspore bank” or just “diaspore bank”. The diaspore bank is very important to ecosystems, because it has the capability to develop a new plant layer after disturbance (Jonsson, 1993; Benschoter, 2006; Shields *et al.*, 2007). Besides, the diaspore bank is also important to the conservation of endemic, rare or endangered species (Jonsson, 1993; Eckstein, 2006; Cailliau & Price, 2007) and may be considered a biodiversity reservoir or genetic memory for many species living in temporarily available habitats (During, 2001; Hock *et al.*, 2008; Smith, 2013).

To our knowledge, Furness & Hall (1981) were the first to discuss the bryophyte diaspore bank. Since then, there has been a gradual increase in research interest in this subject. However, much still remains to be done, because we do not have a deep enough understanding of the ecological role of the bryophyte diaspore bank. Moreover, much less is known about the bryophyte diaspore bank than about the seed bank.

According to our data, research has been carried out on the bryophyte diaspore bank in several types of woods: Mediterranean beech and oak woods (*Fagus sylvatica* L. and *Quercus pubescens* Willd.) near Barcelona in Spain (During *et al.*, 1987); holm oak woods (*Quercus ilex* L.) in France (Hébrard, 2001); Malaysian mountain rainforests (Bisang *et al.*, 2003); Norway spruce forests (*Picea abies* (L.) H. Karst.) in Northwestern Sweden (Jonsson, 1993); mixed-wood forests (red spruce, *Picea rubens* Sarg. and white birch, *Betula papyrifera* Marshall, among others) in Canada (Ross-Davis & Frego, 2004); broadleaf and coniferous woods in Canada (Caners *et al.*, 2009); and Brazilian tropical rain forests (Maciel-Silva *et al.*, 2012). But there are no papers about the bryophyte diaspore bank of Atlantic deciduous forests such as the beech forests that form the object of the present study.

Papers covering both the bryophyte diaspore bank and above-ground bryophytes are even scarcer. Most articles merely mention similarities or differences between the two ecosystem compartments, and very few undertake a systematic comparison. A few exceptions to this are, for instance, During & ter Horst (1983), During *et al.* (1987), Jonsson (1993) and Rydgren & Hestmark (1997).

The bryophyte diaspore bank is of considerable interest because it plays an important role in the total biodiversity of ecosystems. Not all the species which are living in a particular site are always represented in the diaspore bank of that place, and the diaspore bank may have species that are not growing above ground at that particular moment (During, 1997; Cailliau & Price, 2007). Several studies demonstrate that some species may be commonly found below ground, even though they are not observed above ground, either in the vicinity or in a much larger territory (During *et al.*, 1987; Hébrard, 2001; Ederra *et al.*, 2012). Even more amazing is the case of some samples of soil from a Zimbabwean savannah, where

several species not previously known in the country, or even in Africa, appeared in culture, and one of them was newly described (During & Moyo, 1999; Zander & During, 1999; During, 2007). As Zander & During (*loc. cit.*) state, new species are there and contribute to biodiversity; we only have to uncover them.

There are also differences between the morphology and life strategies of species from the bryophyte diaspore bank and from above-ground species: the bryophyte diaspore bank usually contains a higher proportion of acrocarpous colonist species, with a considerable production of gemmae or small spores, while in the above ground vegetation the pleurocarpous perennial species are predominant (During *et al.*, 1987; Jonsson, 1993; During, 2001).

During the last seven years we have been simultaneously studying the bryophyte diaspore bank and the above-ground bryophyte flora of several beech forests from Navarra (Northern Spain), as an example of Atlantic deciduous woods, in order to describe and compare their characteristics. Many questions arise: have the diaspore bank and the above-ground vegetation the same bryoflora? If not, which one of these two ecological compartments is the richest and to what extent are they different? The most frequent species, are the same in the diaspore bank and in the above-ground bryoflora? Are the diaspore banks of the different beech forests equally rich? How can some species have arrived in a diaspore bank? Are the colonist species really the most abundant in the diaspore bank, in contrast with the perennials, which are said to be the most important in the above-ground vegetation? The aim of this paper is to report on the specific composition of these two ecological compartments, comparing their main characteristics and suggesting or giving some answers to those questions.

## METHODS

### Study areas

Our work was carried out in nine beech forests in Navarra (Northern Spain) (Fig. 1), which belong to different phytosociological associations of the class *Querc-Fagetea* Br.-Bl. & Vlieger *in* Vlieger 1937 and have some distinguishing features (Rivas Martínez *et al.*, 2001; Gobierno de Navarra, 2014a):

a) Bértiz, Oroquieta and Quinto Real belong to the association *Saxifrago hirsutae-Fagetum sylvaticae* Br.-Bl. 1967 *em.* Rivas-Martínez, Bascónes, T.E. Díaz, Fernández-González & Loidi 1991 (ShF from now on); they occur on acidic substrata, are located in northern Navarra and receive high precipitation (more than 1600 mm per year). This association is included in the alliance *Ilici-Fagion* Br.-Bl. 1967, order *Quercetalia roboris* Tüxen 1931.

b) Urbasa, S. Miguel de Aralar, Irati 1 and Irati 2 belong to the sub alliance *Scillo-Fagenion* Oberdorfer *ex* Rivas-Martínez 1973 (SF from now on); they grow on basic or neutral soils, in areas influenced by the Cantabric Sea or the Pyrenees, with precipitation ranging between 1400 and 1600 mm per year. We treat these beech forests at a sub alliance level because they have shown to have very similar floristic composition (Delgado & Ederra, 2010). *Scillo-Fagenion* is included in the alliance *Fagion sylvaticae* Luquet 1926, order *Fagetalia sylvaticae* Pawlowski *in* Pawlowski, Sokolowski & Wallisch 1928.

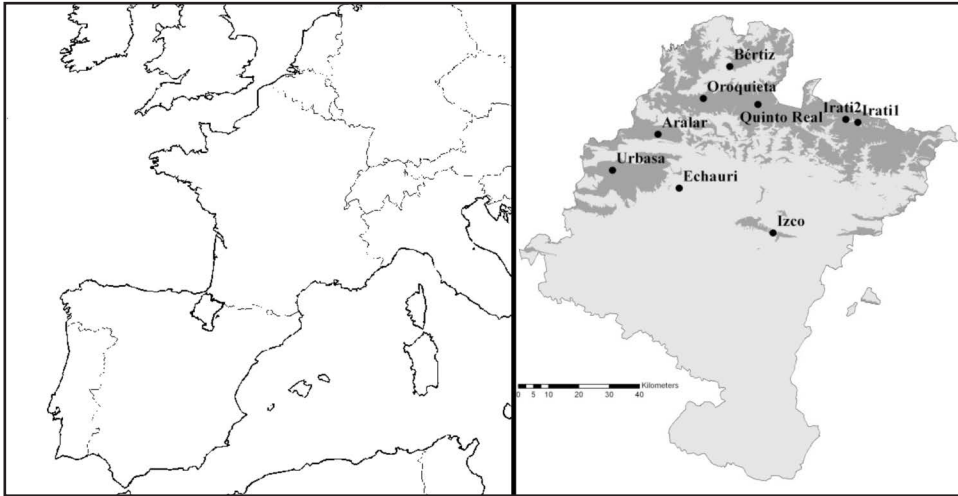


Fig. 1. Map of the beech forests (*Fagus sylvatica*) in Navarra included in this study. Dark-grey colour: current beech distribution area in Navarra.

c) Izco and Echaury belong to the association *Epipactido helleborines-Fagetum sylvaticae* Rivas-Martínez (1962) 1983 (EF from now on); they grow on limestone, are located in the southern part of the beech distribution area in Navarra, in contact with typical Mediterranean vegetation, and annual precipitation ranges from 1000 to 1200 mm. This association belongs to the sub alliance *Epipactido helleborines-Fagenion sylvaticae* Rivas-Martínez, T.E. Díaz, F. Prieto, Loidi & Penas in Rivas-Martínez, Báscones, T.E. Díaz, Fernández-González & Loidi 1991, alliance *Fagion sylvaticae* and order *Fagetalia sylvaticae*.

All these beech forests except Izco and Echaury are included in areas of conservation as SAC (Special Area of Conservation in Natura 2000 network) or SCI (Site of Community Importance) and each one has its own Management Plan approved or under development (Gobierno de Navarra, 2014b). In general, the exploitation of natural resources is allowed, but we always chose areas as natural as possible to take the samples, avoiding places with signs of cutting or grazing. In this way, we tried to study just the best examples of stable forest habitats.

### Sampling, cultivation and nomenclature

We took cylindrical soil samples to a depth of 10 cm, with a 5 cm diameter soil corer, in each one of the 9 beech forests studied. In order to have representative samples of the whole bryophyte diaspore bank and to enable us to detect the growth of as many bryophyte species as possible, we extracted 64 soil cylinders from every site, 32 in spring and 32 in autumn (bryophytes can disseminate their diaspores at different times of year). Places for soil sampling collections were always selected inside the forests, avoiding surfaces with stones or signs of disturbance.

The soil cores were kept in plastic bags and carried to the laboratory. Once in the lab, the soil cores were dried exposing them to the air and all dead leaves or green elements were removed. Then we ground the soil samples with a

rolling pin and kept them in the fridge (4°C) for a month. A period of low temperature previous to cultivation has demonstrated to be very effective in breaking the dormancy of seeds (Thompson *et al.*, 1997), which makes much better the germination of vascular plants in soil cultures. One of us also confirmed that cold improves a lot the growth of bryophytes (Iglesias Teixeira, 2013) and some authors also stored the soil samples at low temperature for a time, *e.g.* Rydgren & Hestmark (1997) at 2°C for 5 weeks.

After this, the soil samples were spread in layers of 1 cm thick on plastic plates, 12 cm wide and 5.5 cm deep, over a sterile peat layer. The plates were cultivated in a greenhouse, under controlled conditions of temperature (15-25°C), moisture (watered as required so that they were always moist) and light (sunlight in summer plus artificial light in winter). We cultivated a total of 144 plates: 8 for every one of the 9 beech woods and for every season, every plate with about 120 cm<sup>3</sup> of soil.

We also cultivated four additional plates with only the sterile peat layer, to control for the possible existence of airborne spores. No species grew on these sterilized plates, so we decided that all bryophytes germinating in the other plates came from the soil samples and, as no strictly epiphyte or saxicolous bryophytes appeared in the cultures, we took into account all the species growing from the soil samples for further analysis.

The germination of bryophytes was checked monthly for eight or nine months, long enough for most of the species to appear (Iglesias Teixeira, 2013).

At the same time as we took the soil samples, we collected bryophytes in the same nine beech forests, prospecting areas around the sites where the soil cylinders were taken and avoiding disturbed zones, clearings or paths. The bryophytes were collected from all kind of substrates (see the full check-lists in Delgado & Ederra, 2013), but in the present paper we will only consider the terricolous bryophytes, to make comparison with the bryophytes of the diaspore bank possible.

The nomenclature of mosses follows Ros *et al.* (2013); for liverworts Ros *et al.* (2007) was the reference work. Some specimens from the diaspore bank could not be identified at species level so they were classified at genus or family level. For the life strategy categories we follow Dierßen (2001), according to Düring (1992).

## Analyses

Multivariate analysis of the patterns found were performed with Canoco (version 4.5) (ter Braak & Smilauer, 2002). We used DCA (Detrended Correspondence Analysis), which is a useful test to perform an ordination of the beech forests from a presence-absence matrix. This matrix includes all the species in the soil surface of the forests and in their diaspore banks.

Simple linear regression analysis were done with Microsoft Excel 2010.

We also calculated the Jaccard (J) similarity index between the bryophyte diaspore bank and the soil surface bryophytes for each forest according with to the formula:

$$J = 100 c / a + b - c$$

where c is the number of species present in both inventories compared and a and b are the total number of species in each inventory (Margalef, 1986). J index was equally calculated for forest types (ShF, SF, EF), now considering as “inventory” all the species appearing in any forest included in each of the forest types.



Table 1. Bryophytes from the soil surface and from the diaspore bank of the beech forests (*continued*)

LIVERWORTS	ShF						SF								EF				Frequency	
	OS	OD	QS	QD	BS	BD	IIS	IID	I2S	I2D	AS	AD	US	UD	ES	ED	IS	ID	TS	TD
<i>Pellia endiviifolia</i> (Dicks.) Dumort.					C				C	C									33	
<i>Pellia epiphylla</i> (L.) Corda	C		C		C														33	
<i>Plagiochila porelloides</i> (Torrey ex Nees) Lindenb.			P		P		P		P	P		P					P		78	0
<i>Porella arboris-vitae</i> (With.) Grolle							P					P							22	
<i>Riccia</i> sp.															x					11
<i>Scapania aspera</i> Bernet & M. Bernet										C		C							22	
<i>Scapania nemorea</i> (L.) Grolle	P				P				P	P									44	
<b>MOSSES</b>																				
<i>Atrichum undulatum</i> (Hedw.) P. Beauv.	SS	SS	SS	SS	SS	SS	SS	SS	SS	SS	SS	SS	SS						78	55
<i>Barbula unguiculata</i> Hedw.						C										C			22	
Brachytheciaceae		P		P		P		P		P		P		P		P		P	0	100
<i>Brachythecium dieckii</i> (Röll) Ignatov & Huttunen							P		P						P		P		44	
<i>Brachythecium velutinum</i> (Hedw.) Ignatov & Huttunen					P		P			P					P		P		55	
<i>Brachythecium rutabulum</i> (Hedw.) Schimp.			P		P		P		P	P		P		P		P		P	89	0
<i>Bryum argenteum</i> Hedw.					C	C		C							C				11	33
<i>Bryum dichotomum</i> Hedw.		C			C	C													11	22
<i>Calliergonella cuspidata</i> (Hedw.) Loeske					P				P										22	
<i>Calliergonella lindbergii</i> (Mitt.) Hedenäs									P										11	
<i>Campyliadelphus chrysophyllum</i> (Brid.) R.S. Chopra													P						11	
<i>Campylidium calcareum</i> (Crundw. & Nyholm) Ochyra															P				11	
<i>Campylium stellatum</i> (Hedw.) Lange & C.E.O. Jensen									P										11	
<i>Campylopus introflexus</i> (Hedw.) Brid.	P	P		P		P		P		P		P							11	66
<i>Campylopus pyriformis</i> (Schultz) Brid.						C													11	
<i>Ctenidium molluscum</i> (Hedw.) Mitt.			P		P		P			P		P		P		P			78	0
<i>Dicranella heteromalla</i> (Hedw.) Schimp.	C	C	C	C	C	C		C		C		C		C					33	78
<i>Dicranella howei</i> Renaud & Cardot				C		C		C	C										11	33
<i>Dicranella varia</i> (Hedw.) Schimp.						C		C				C		C		C		C	66	
<i>Dicranum scoparium</i> Hedw.	P		P		P				P	P							P		66	
<i>Didymodon fallax</i> (Hedw.) R.H. Zander															C		C		22	
<i>Didymodon insulanus</i> (De Not.) M.O. Hill			C						C	C		C					C		55	
<i>Didymodon</i> sp.						C												C	22	





Table 1. Bryophytes from the soil surface and from the diaspore bank of the beech forests (*continued*)

LIVERWORTS	ShF						SF								EF				Frequency		
	OS	OD	QS	QD	BS	BD	IIS	IID	I2S	I2D	AS	AD	US	UD	ES	ED	IS	ID	TS	TD	
<i>Plagiomnium undulatum</i> (Hedw.) T.J. Kop.			P		P		P		P						P				55		
<i>Plagiopus oederianus</i> (Sw.) H.A. Crum & L.E. Anderson													LS						11		
<i>Plagiothecium nemorale</i> (Mitt.) A. Jaeger			P		P						P								33		
<i>Plagiothecium undulatum</i> (Hedw.) Schimp.					P														11		
<i>Pleurozium schreberi</i> (Willd. ex Brid.) Mitt.					P														11		
<i>Pogonatum aloides</i> (Hedw.) P. Beauv.	P		P		P														33		
<i>Pogonatum nanum</i> (Hedw.) P. Beauv.					C														11		
<i>Pogonatum urnigerum</i> (Hedw.) P. Beauv.	C																		11		
<i>Pohlia andalusica</i> (Höhn.) Broth.						C														11	
<i>Pohlia</i> sp.1				x		x		x		x			x							66	
<i>Pohlia</i> sp.2		x																		11	
<i>Polytrichum formosum</i> Hedw.	P	P	P	P	P	P	P	P	P	P	P	P	P	P				P	89	78	
<i>Polytrichum piliferum</i> Hedw.	P																			11	
<i>Pseudophemerum nitidum</i> (Hedw.) Loeske		C		C	C	C		C		C		C		C		C		C	11	100	
<i>Pseudoscleropodium purum</i> (Hedw.) M. Fleisch.					P				P				P		P					44	
<i>Pseudotaxiphyllum elegans</i> (Brid.) Z. Iwats.					P															11	
<i>Ptychostomum capillare</i> (Hedw.) Holyoak & N. Pedersen											C		C		C		C			44	
<i>Ptychostomum pseudotriquetrum</i> (Hedw.) J.R. Spence & H.P. Ramsay			P																	11	
<i>Ptychostomum rubens</i> (Mitt.) Holyoak & N. Pedersen		C		C		C		C		C		C		C		C		C	0	100	
<i>Rhizomnium punctatum</i> (Hedw.) T.J. Kop.			LS		LS															22	
<i>Rhytidiadelphus loreus</i> (Hedw.) Warnst.	P		P		P		P				P									55	
<i>Rhytidiadelphus squarrosus</i> (Hedw.) Warnst.					P															11	
<i>Rhytidiadelphus triquetrus</i> (Hedw.) Warnst.	P		P		P		P		P		P		P				P			89	0
<i>Sciuro-hypnum populeum</i> (Hedw.) Ignatov & Huttunen									P											11	
<i>Sphagnum quinquefarium</i> (Braithw.) Warnst.					LS															11	
<i>Sphagnum</i> sp.		LS				LS														22	
<i>Thuidium assimile</i> (Mitt.) A. Jaeger													P							11	
<i>Thuidium delicatulum</i> (Hedw.) Schimp.			P		P	P														22	11
<i>Thuidium recognitum</i> (Hedw.) Limdb.													P							11	

Table 1. Bryophytes from the soil surface and from the diaspore bank of the beech forests (*continued*)

LIVERWORTS	ShF						SF								EF				Frequency	
	OS	OD	QS	QD	BS	BD	IIS	IID	I2S	I2D	AS	AD	US	UD	ES	ED	IS	ID	TS	TD
<i>Thuidium tamariscinum</i> (Hedw.) Schimp.	P		P		P		P		P		P	P	P	P		P			100	11
<i>Tortella tortuosa</i> (Hedw.) Limpr.			P				P				P		P				P		55	
<i>Tortula acaulon</i> (With.) R.H. Zander			AS											AS		AS		AS		44
<i>Tortula muralis</i> Hedw.					C	C										C		C	11	33
<i>Tortula subulata</i> Hedw.														C		C			22	
<i>Tortula truncata</i> (Hedw.) Mitt.			AS			AS												AS		33
<i>Trichodon cylindricus</i> (Hedw.) Schimp.		C		C		C		C		C		C		C		C		C	0	100
<i>Weissia controversa</i> Hedw.		C	C	C	C	C		C		C		C		C	C	C		C	33	100
<i>Weissia longifolia</i> Mitt.														SS					11	

ShF, *Saxifraga hirsutae-Fagetum*; SF, *Scillo lilio-hyacinthi-Fagenion*; EF, *Epipactido helleborines-Fagetum*; OS, from the soil surface of Oroquieta; OD, from the diaspore bank of Oroquieta; QS, from the soil surface of Quinto Real; QD, from the diaspore bank of Quinto Real; BS, from the soil surface of Bértiz; BD, from the diaspore bank of Bértiz; IIS, from the soil surface of Irati 1; IID, from the diaspore bank of Irati 1; I2S, from the soil surface of Irati 2; I2D, from the diaspore bank of Irati 2; AS, from the soil surface of Aralar; AD, from the diaspore bank of Aralar; US, from the soil surface of Urbasa; UD, from the diaspore bank of Urbasa; ES, from the soil surface of Echauri; ED, from the diaspore bank of Echauri; IS, from the soil surface of Izco; ID, from the diaspore bank of Izco; TS, from the soil surface of all the beech forests; TD, from the diaspore bank of all the beech forests; P, perennial; C, colonist; LS, long-life shuttle; AS, annual shuttle; SS, short-life shuttle; F, fugitive; x, unknown life strategy.

The total number of bryophytes from the above-ground vegetation of the nine beech forests studied is 103 as a whole; as usual in Atlantic woods, there are quite a lot of liverworts: 26 species, which account for 25%. In the diaspore bank the total number of species is 40; but there are only 6 liverworts, that is, 15%. The floristic richness values in both ecological compartments in each beech forest are varied, with a certain trend towards higher values in the ShF forests and lower in the EF ones.

The similarity between above-ground and diaspore bank bryophyte species composition was very low for each beech forest pair studied if all the species are taken into account: the Jaccard index values (Table 2) ranges from 3 to 18. However, they rise considerably when only the most frequent species (those with frequency higher than 75%) are considered, to reach a value of 69 if all the forests are considered as a whole. In parallel, J values are very low for the beech forests grouped in phytosociological communities and considering all the species (from 7 to 16), but again, with the most frequent species, J values rise considerably, up to 57 in ShF beech forests.

As a complementary way to understand the differences in specific composition between the diaspore bank and the above-ground vegetation we present a complete matrix of Euclidean distances (Table 3). The lowest distances (closest resemblances) are always between samples of the same ecological compartment; this is, any sample from a diaspore bank is always more similar to anyone else from another diaspore bank than to anyone else from the above-ground vegetation, and the same applies to the samples from the above-ground vegetation. On the other hand, the highest distances (highest differences) are nearly always between any sample and the forests as a whole, probably because of the importance that the absences (zeroes) have in the Euclidean distances calculation.

Table 2. Floristic richness, D/S values (number of species in the diaspore bank/number of species in the corresponding above-ground vegetation) and Jaccard similarity index values for the beech forests or the different pairs compared

	ShF						SF								EF				Totals and frequency > 75%	
	OS	OD	QS	QD	BS	BD	IIS	IID	I2S	I2D	AS	AD	US	UD	ES	ED	IS	ID	TS	TD
Floristic richness	27	19	46	16	72	30	18	19	28	13	31	18	27	16	22	13	22	15	103	40
D/S	0,70		0,35		0,42		1,06		0,46		0,58		0,59		0,59		0,68		0,39	
Number of species with frequency > 75%	8	8	13	9	13	9	11	9	12	9	13	9	11	9	8	7	12	7	13	9
Jaccard similarity index (all species)	18		9		15		9		5		11		5		6		3		16	
Jaccard similarity index (frequent species)	33		29		47		18		11		22		11		15		6		69	
Total species / phytosociological communities	ShFS: 86			ShFD: 36			SFS: 48				SFD: 23				EFS: 29		EFD: 18			
D/S	0,42						0,48						0,58							
Number of species with frequency > 75% / phytosociological communities	ShFS: 13			ShFD: 9			SFS: 13				SFD: 9				EFS: 12		EFD: 7			
Jaccard similarity index (all species) / phytosociological communities	16						9						7							
Jaccard similarity index (frequent species) / phytosociological communities	57						22						12							

ShFS, bryophytes from the soil surface of the *Saxifraga hirsutae-Fagetum*; ShFD, bryophytes from the diaspore bank of the *Saxifraga hirsutae-Fagetum*; SFS, bryophytes from the soil surface of the *Scillo liliohyacinthi-Fagenion*; SFD, bryophytes from the diaspore bank of the *Scillo liliohyacinthi-Fagenion*; EFS, bryophytes from the soil surface of the *Epipactido helleborines-Fagetum*; EFD, bryophytes from the diaspore bank of the *Epipactido helleborines-Fagetum*. See the meaning of the other initials in the legend to Table 1.

To clarify how the low similarity for pairs worked if the beech forests and their diaspore banks altogether were considered, we made the multivariate analysis DCA (Detrended Correspondence Analysis) taking into account the presence/absence of all species (Fig. 2). Eigenvalues of axis 1 (horizontal) and axis 2 (vertical) are 0,7018 and 0,1826 respectively; the percentages of variation explained are 31% for axis 1 and 8% for axis 2. Axis third and fourth are almost uninformative, with eigenvalues of 0,1177 and 0,0713 and percentages of variation explained of 5,2% and 3,2% respectively. In accordance with the clear and great importance of axis 1, DCA displays the ordination of the inventories clearly split in two groups with respect to this axis: the beech forests with the records of all the surface species are to the left and the results with the diaspore bank species are to the right. An additional DCA was made taking into account only the species that reach a frequency higher than 75%, obtaining similar results.

As one of the more reported differences in the literature between the above-ground and the diaspore bank bryophytes is related with the life strategies, we calculated the percentages of all the strategies, as they appear in Table 1. Fig. 3 displays the percentages of only the colonist and perennial species that are in the surface and in the diaspore bank of all beech forests, one by one and in

Table 3. Matrix of Euclidean distances between all samples. There are highlighted in bold (with asterisks) and highest (without asterisks) distances between samples; in italics those corresponding to the above-ground vegetation, in non-italics those from the diaspore bank

	OS	OD	QS	QD	BS	BD	IIS	IID	I2S	I2D	AS	AD	US	UD	ES	ED	IS	ID	ShFS	ShFD	SFS	SFD	EF5	EFD	TS	TD	
OS	0																										
OD	5,7	0																									
QS	6,1	7,1	0																								
QD	5,9	<b>3,6*</b>	7,2	0																							
BS	7,7	8,4	6,3	8,6	0																						
BD	7	4,6	<b>7,9</b>	4	<b>8,7</b>	0																					
IIS	<b>5,6*</b>	5,7	5,8	5,3	7,7	6,5	0																				
IID	6,2	4	7,3	<b>2,2*</b>	8,5	3,3	5,6	0																			
I2S	5,7	6,4	6	6	7,5	7,1	<b>4,5*</b>	6,2	0																		
I2D	5,8	3,7	7,1	<b>2,2*</b>	8,5	4,1	5,2	2,4	6,1	0																	
AS	<b>5,6*</b>	6,5	<b>5,2*</b>	6,4	7,1	7,3	4,3	6,5	4,8	6,3	0																
AD	5,9	3,9	7,1	2,4	8,5	3,7	5,3	<b>1,7*</b>	6,2	<b>2,2*</b>	6,2	0															
US	6,3	6,3	6,2	6,1	8,2	7,1	4,6	6,3	5,4	6	4,7	6,1	0														
UD	6,2	4,1	7,2	2,8	8,6	4,5	5,5	3	6,3	<b>2,2*</b>	6,4	2,8	6,2	0													
ES	6,4	6,1	6,5	5,8	8	6,8	4,5	5,9	5,3	5,6	5,2	5,6	5,2	5,8	0												
ED	6,3	4,2	7,4	3,9	8,5	4,6	5,4	3,7	6,2	3,5	6,5	3,9	6,2	3,3	5,6	0											
IS	5,7	6,1	6	5,8	8	6,9	<b>3,7*</b>	6,1	4,7	5,6	<b>4,1*</b>	5,8	<b>4,3*</b>	5,8	3,7	5,7	0										
ID	6,5	4,2	7,4	3,9	<b>8,7</b>	4,6	5,6	4	6,4	3,7	6,5	3,9	6,3	3,3	5,6	2,8	5,9	0									
ShFS	7,6	9,0	6,4	9,2	<b>3,9*</b>	9,3	8,5	9,2	8,3	9,2	7,6	9,1	8,6	9,3	8,9	9,3	8,5	<b>9,4</b>	0								
ShFD	7	4,1	<b>7,9</b>	4,5	<b>8,7</b>	<b>2,4*</b>	6,9	4,1	7,3	4,8	7,4	4,5	7,4	4,7	7,1	5	7,2	4,8	9,3	0							
SFS	7,1	7,7	6,1	7,5	7,4	8,3	5,6	7,6	4,6	7,6	<b>4,2*</b>	7,5	4,7	7,7	6,1	7,7	5,6	7,7	8	<b>8,4</b>	0						
SFD	6,3	4,2	7,3	2,6	8,5	3,9	5,7	<b>2*</b>	6,4	3,2	6,5	<b>2,2*</b>	6,5	2,6	6,1	4	6,2	4	9,2	4,1	7,6	0					
EF5	6,3	6,5	5,9	6,2	7,8	7,1	4,1	6,3	4,8	6	4,5	6,1	4,9	6,2	<b>2,6*</b>	6,2	<b>2,6*</b>	6,2	8,5	7,4	5,5	6,5	0				
EFD	6,7	4,6	7,6	4,2	<b>8,7</b>	4,5	5,8	4,1	6,6	4,1	6,7	4,2	6,5	3,7	5,8	<b>2,2*</b>	6,2	<b>1,7*</b>	<b>9,4</b>	4,7	7,9	4,1	6,4	0			
TS	<b>8,7</b>	<b>10</b>	7,5	<b>10</b>	5,6	<b>10,1</b>	<b>9,2</b>	<b>10</b>	<b>8,7</b>	<b>10,1</b>	<b>8,5</b>	<b>10</b>	<b>8,7</b>	<b>10,2</b>	<b>9</b>	<b>10,2</b>	<b>9</b>	<b>10,2</b>	<b>9</b>	<b>10,3</b>	<b>4,2*</b>	<b>10,1</b>	7,3	<b>10</b>	<b>8,6</b>	<b>10,3</b>	0
TD	7,1	4,6	<b>7,9</b>	4,9	<b>8,7</b>	3,2	7,1	4,6	7,5	5,2	7,4	4,7	7,5	4,9	7,2	5,2	7,3	5	9,3	<b>2*</b>	<b>8,4</b>	4,11	7,5	4,7	<b>10,1</b>	0	

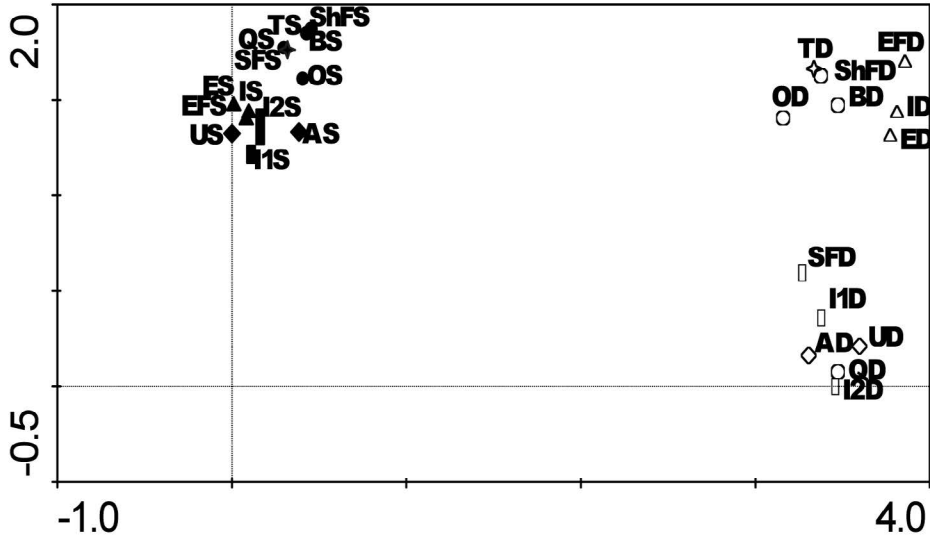


Fig. 2. DCA ordination with all the above-ground (black symbols) and diaspore bank (empty symbols) bryophytes. Horizontal axis (Axis 1): Eigenvalue 0,7018; % variance explained 31%. Vertical axis (Axis 2): Eigenvalue 0,1826; % variance explained 8%. Black symbols are above-ground samples; empty symbols are diaspore bank samples. See the legend to Tables 1 and 2 for the meaning of the initials.

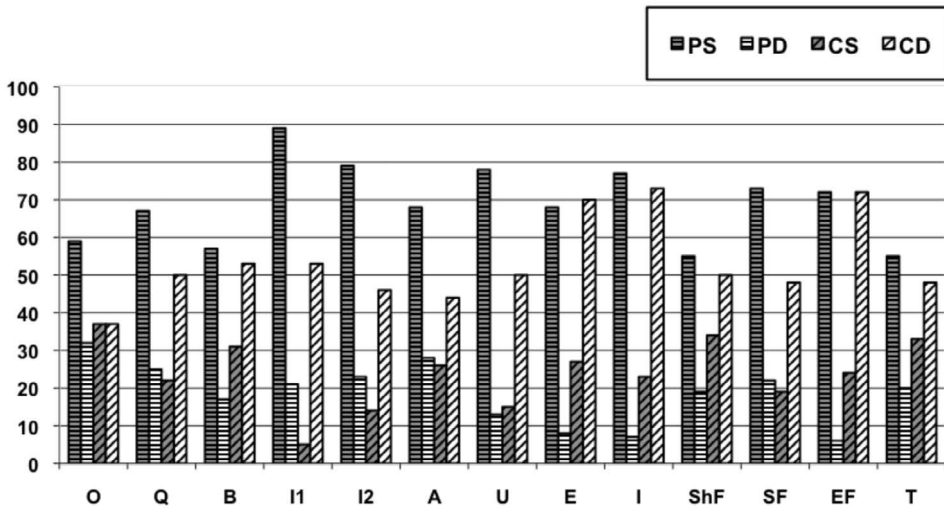


Fig. 3. Percentages of perennial and colonist species in the beech forests studied and in their diaspore banks: separately, by phytosociological communities and as a whole. PS, perennial species in the terricolous bryoflore; PD, perennial species in the diaspore banks; CS, colonist species in the terricolous bryoflore; CD, colonist species in the diaspore banks. See Tables 1 and 2 for an explanation of the initials on the horizontal axis.

Table 4. Differences between percentages of colonist and perennial species in the diaspore banks and in the above-ground vegetation tested with the Tukey's pairwise test following ANOVA

	<i>PS</i>	<i>PD</i>	<i>CS</i>
PD	***		
CS	***	n.s.	
CD	**	***	***

\*\*\*,  $P < 0,001$ ; \*\*,  $0,001 < P < 0,01$ ; n.s., not significant.

groups according to phytosociological communities. The percentages of fugitive, annual shuttle, short-life shuttle and long-life shuttle species have been left out as they are not representative (see how scarce they are in Table 1). The percentages of perennial species are always higher in the terricolous bryophytes than in the diaspore banks, while on the contrary, the percentages of colonist species are considerably higher in the diaspore banks than in the terricolous bryoflora, except for the Oroquieta beech forest, where values are the same. The differences between percentages of colonist or perennial species in the diaspore banks and in the above-ground vegetation are always statistically very significant ( $P < 0,001$ , Table 4).

## DISCUSSION

The floristic richness in the bryophyte diaspore bank of the beech forests studied was 40, which represents a large number of species. In fact, as far as we know, this is higher than that of any other kind of plant community. For instance, in xerophitic beech woods near Barcelona the diaspore bank has 34 species (During *et al.*, 1987); in Antarctic fellfield soils, 14 species (Smith, 1987); in Swiss cultivated fields, 15 species (Bisang, 1996); in Norwegian *Picea* forests, 18 species (Rydgren & Hestmark, 1997); in soils four years after a mining disaster in Spain, 15 species (Ordóñez *et al.*, 2003); in soil and litter of an urban bushland in Western Australia, 15 species (Biggs & Wittkuhn, 2006); in Brazilian tropical rain forests, 22 species (Maciel-Silva *et al.*, 2012); and 17 species in the Mojave Desert (Smith, 2013). Only in boreal forests of conifers in Sweden (Jonsson, 1993) were there such a variety of flora (40 species). Beech forests are generally ecosystems with high diversity (Delgado & Ederra, 2013) and we think it is logical that their diaspore banks have a lot of species, but we also consider that there might be other reasons for this high richness in the diaspore bank. For instance, we have collected and studied more soil per site than in the studies mentioned above, *e.g.*, 10 cm<sup>3</sup> per plot in During *et al.* (1987) or 78 cm<sup>3</sup> per culture pot in Rydgren & Hestmark (1997); besides, we have maintained our cultures 8-9 months, which is quite more time than in other studies, *e.g.*, 4-5 months in During *et al.* (1987), 160 days in Smith (1987), etc., and maybe some species have simply managed to emerge due to the long period of cultivation.

The number of species in the diaspore bank is smaller than the number of species in the above-ground vegetation; moreover, there is even a positive correlation between the two values. Our study found a strong correlation between the floristic richness in the diaspore bank and the above-ground vegetation of the Atlantic beech forests (except for Irati 2), both one by one or taken in groups: the higher the number of species in the above-ground vegetation, the higher the

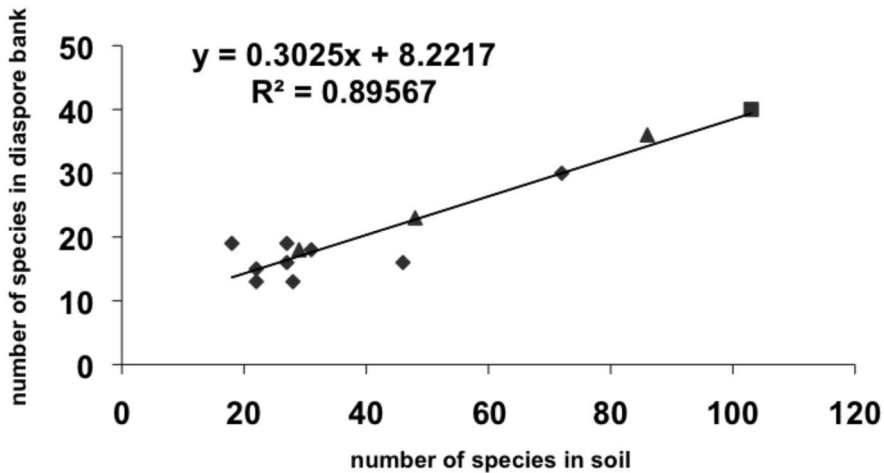


Fig. 4. Simple linear regression between the total number of bryophyte species from the above-ground vegetation (soil) and the number in the corresponding diaspore bank. Values are included for each beech forest (◆), for groups of beech forests by phytosociological communities (▲) and for the beech forests altogether (■).

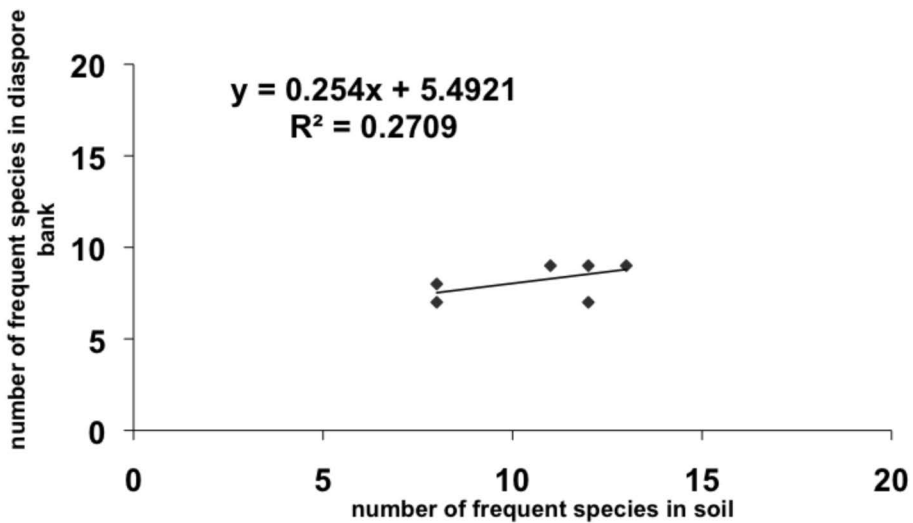


Fig. 5. Simple linear regression between the total number of the most frequent bryophyte species from the above-ground vegetation (soil) (> 75%) and the number in the corresponding diaspore bank. Values are included for each beech forest, for groups of beech forests by phytosociological communities and for the beech forests altogether. All of them are represented by ◆ because there are a lot of coincident values; for instance, the point (13,9) is repeated six times (cf. Table 2).

number of species in the diaspore bank (Table 2 and Fig. 4). However, the correlation was lost if only the most frequent species (more than 75%: 20 in total, 13 in the above-ground vegetation and 9 in the diaspore bank) were taken into account (Table 2 and Fig. 5). This can mean that both the diaspore bank and

the above-ground vegetation of each beech forest tend to share most of the frequent species, regardless of their total number of species. Both the beech forests and the diaspore banks are ecological compartments that work the same as many plant communities: there are few species which are very frequent and a lot of species which are infrequent (Braun-Blanquet, 1979; Rydgren & Hestmark, 1997). In our study the frequent species cause the resemblance between the diaspore bank and the above-ground vegetation (see values of J index in Table 2) and the loss of correlation between the two compartments (Fig. 5), whereas the infrequent species turn out to be the cause of the correlation between the number of species in every beech forest and their diaspore banks.

The acidophytic beech forests (Bértiz, Oroquieta and ShF group) and the beech forests as a whole have the richest bryophyte diaspore banks (Table 2). Nevertheless, the results are the exact opposite when the ratio D/S (number of species in the diaspore bank) / (number of species in the corresponding above-ground bryoflora) is calculated (Table 2); with the exception of Oroquieta, now the acidophytic beech forests and the whole forests (Total) are indeed the poorest. The reason for this could be just the high diversity of the *Saxifraga hirsutae-Fagetum* compared with that in the other kinds of beech forests. It could be said that the diaspore banks of the acidophytic beech forests, although rich in absolute number of species, may be less capable of developing and recovering their terricolous bryoflora than the beech forests belonging to other phytosociological communities. This fact may contribute (of course, along with other reasons like the acidity of the substrate or the steep slopes) to the difficulties that the *Saxifraga hirsutae-Fagetum* have to recover from disturbances (Gobierno de Navarra, 2014a).

The floristic composition of the diaspore bank of the beech forests is very different from that of the above-ground bryophyte community, as can be deduced from Table 1, from the values of Jaccard index in Table 2 or Euclidean distances in Table 3 and from the ordination diagram in Fig. 2. This is a general result, widely shared with many other papers (*e.g.*, Smith, 1987; Bisang, 1996; Rydgren & Hestmark, 1997; Ghorbani *et al.*, 2003; Cailliau & Price, 2007), although some authors find a more similar flora composition than we do (*e.g.*, Jonsson, 1993; Maciel-Silva *et al.*, 2012). Jaccard similarity indexes increase considerably if only the species with frequency higher than 75% are taken into account (Table 2). But even in this case the difference in flora composition is remarkable, as can be seen in Fig. 6: nine out of the 20 more frequent species are found both in the diaspore bank and in the over-ground bryoflora, but only *Fissidens taxifolius* and *Polytrichum formosum* may be regarded as frequent in both compartments; the other seven species are more frequent either in the diaspore bank or in the above-ground vegetation.

Some authors (During & ter Horst, 1983; During *et al.*, 1987; Bisang *et al.*, 2003) state that all the species from the diaspore bank end up appearing in the above-ground vegetation if wider surfaces are studied. We partly agree with their opinion, since quite a lot of the species which appear in the diaspore bank, and not in the above-ground vegetation of the beech forests, are common along paths or in clearings, habitats where we took no samples in the present study; this is the case with, say, *Barbula unguiculata*, *Ptychostomum rubens*, *Tortula acaulon* or *T. truncata*, which would certainly have appeared among the above-ground bryoflora of the beech forests if we had studied suitable environments. However, the appearance of some species in the diaspore bank of our studied areas is hard to explain, given that their suitable environments or their previously known records are sometimes tens or even hundreds of kilometers away. This raises the



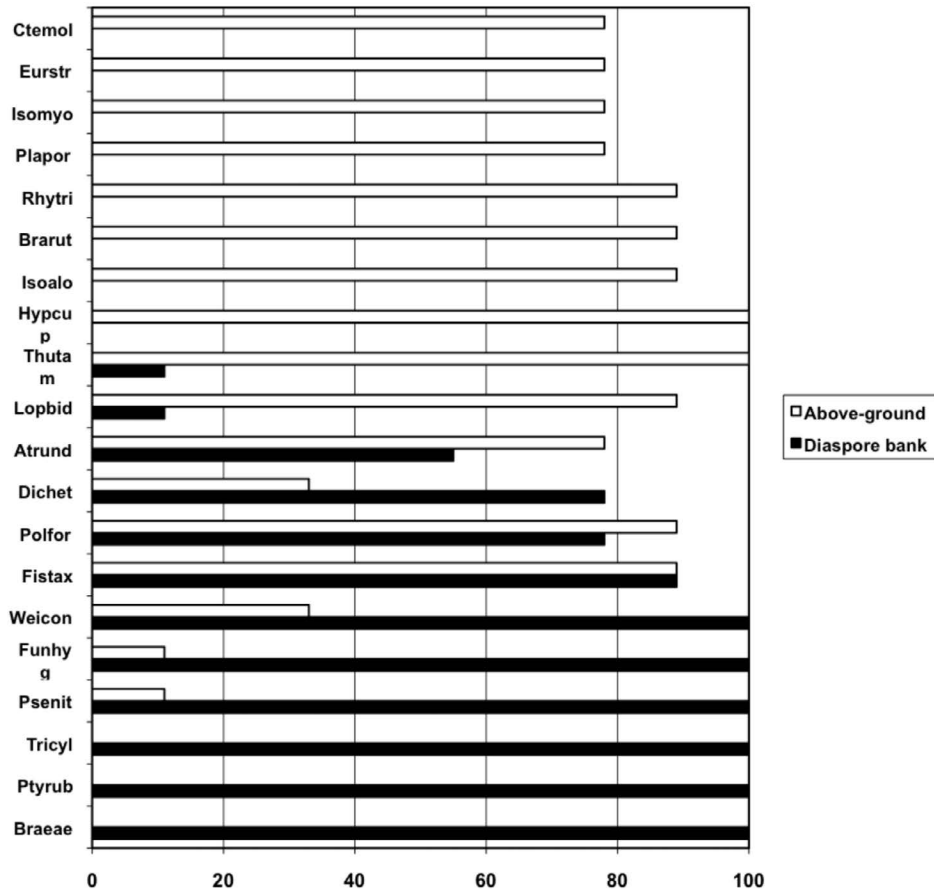


Fig. 6. Frequency of the most frequent species in the above-ground bryoflore (more than 75%) and/or in the diaspore bank. In the vertical line, species are represented by the first three letters of the generic name followed by the first three letters of the specific name; to check the names, see Table 1.

question: how have the diaspores of these species arrived and been incorporated into the diaspore bank of the beech forests? We think that, of course, a lot of species may arrive by short distance dispersal; but some others, for instance some uncommon species such as *Pohlia andalusica* or *Trichodon cylindricus*, only known in Navarra through their appearance in the beech forest diaspore bank (Ederra *et al.*, 2012), and *Sphagnum* sp., away from a suitable environment, must have been transported over a long distance. Wind could be the main transport agent, as is known to be the case in the Antarctic (Smith, 1987; Marshall & Convey, 1997), where the diaspore bank contains species not previously known in that continent and whose diaspores were trapped in special devices arranged to capture air-borne particles. Long-distance dispersal is well known and documented (Miller & McDaniel, 2004; Muñoz *et al.*, 2004; Frahm, 2012) and may happen everywhere either by the wind or other agents such as sheep (Pauliuk *et al.*, 2011). And of course, there is the evidence of long-distance dispersal

concerning the diaspore bank of a Zimbabwean savannah (During & Moyo, 1999; Zander & During, 1999; During, 2007) that we have already mentioned in the Introduction. Therefore, it should not be considered odd that species which are not in the neighboring area do appear in the diaspore bank.

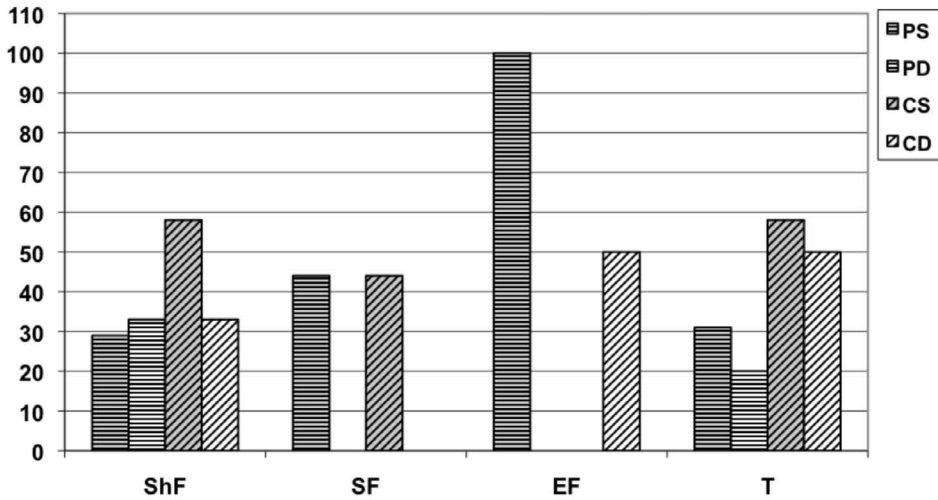
Besides the long-distance dispersal, the presence of some species in the diaspore bank may be due to the great survival capacity of the propagules or gametophyte fragments: Clymo & Duckett (1986) found new shoots of *Sphagnum* arising as innovations growing from buried stems or spores in culture of samples which were 25-60 years old; Dyer & Lindsay (1992) suggested that diaspores of some weedy bryophytes might have survived deep in the soil of some woods in North Carolina (USA) for more than 100 years; During & Moyo (1999) stated that diaspores can remain for a long time in the soil and that they can even survive burning events; Hebrard (2001) also said that perennial bryophytes sprout from apparently dead plants. There is also the extraordinary regeneration of Little Ice Age bryophytes in Canada several centuries later (La Farge *et al.*, 2013). We have also seen small pieces of Hypnaceae stems, brown and apparently dead, sprouting freely after several months of cultivation.

It is worth noting the presence of *C. introflexus* in the diaspore bank of six out of the nine studied beech forests and in the above-ground vegetation of only one beech forest. *C. introflexus* is a well-known alien species, which has been invasive in several European countries since 1941 (Hassel & Söderström, 2005). Essl *et al.* (2013) point out that, like other aliens, it is normally found in habitats with anthropogenic disturbance regime, and its occurrence in natural or near-natural environments is very uncommon; but according to our results, we have to conclude that *C. introflexus* is nowadays so well-settled as to become a regular species of the beech forests diaspore bank. Therefore, *C. introflexus* must be considered fully naturalized.

One of the clearest differences between the diaspore bank and the above-ground vegetation is connected with the life strategies (Fig. 3). The colonists dominate in the diaspore bank, while in the above-ground vegetation the best represented strategy is the perennial one, being the differences highly significant (Table 4). Opinions on this subject are unanimous in all the references consulted. It is interpreted as the consequence of the main role of the diaspore bank, which is to make the recovery of a layer of bryophytes easier following disruption, disturbance or destruction of the formerly extant vegetation. As colonist species are the ones which are best adapted to settle and grow in such environments, it is logical that they are predominant in the diaspore bank.

The difference between the percentages of colonist and perennial species is lower in the *Saxifrago hirsutae-Fagetum* group than in the other phytosociological communities (Fig. 3). This fact can be also seen in the beech forests altogether (Fig. 3), because the higher floristic richness in the ShF has an effect on the values of all the beech forests considered as a whole. The representation of the percentages of perennials and colonists liverworts and mosses separately (Fig. 7) highlights that the lower difference observed in the ShF (and in the beech forests altogether) is due to the values of the colonist liverworts. Indeed, in the ShF (and in the beech forests altogether, though less striking) the percentage of colonist liverworts is higher in the above-ground vegetation than in the diaspore bank. The same happens in the SF, where there is a complete lack of colonist liverworts in their diaspore banks. However, as the predominance of colonists in the mosses of the diaspore bank is very clear, when all the bryophytes are considered together, this predominance remains.

### Liverworts



### Mosses

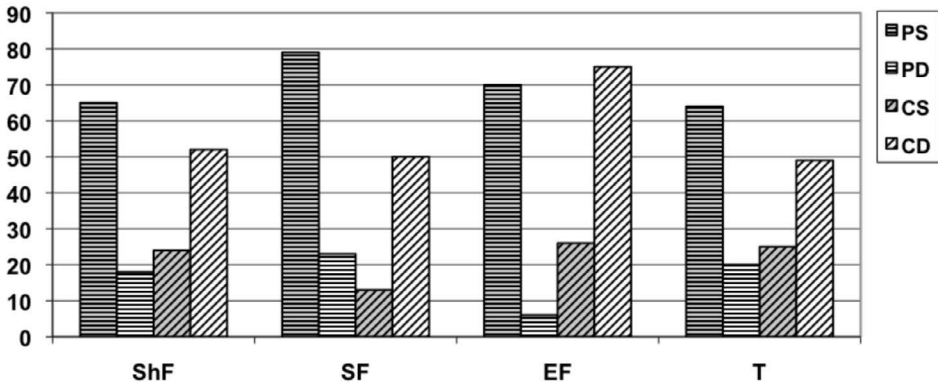


Fig. 7. Percentages of perennial and colonist species in the diaspore bank and in the above-ground vegetation in the beech forests grouped in phytosociological communities and as a whole. Above, liverworts; below, mosses. See the meaning of initials in Table 2 and Fig. 3.

It is interesting to pay attention to the absolute numbers and percentages of liverworts and mosses living in the above-ground vegetation and in the diaspore bank of the ShF. In the above-ground vegetation: 24 liverworts (28%) and 62 mosses (72%); in the diaspore bank: 3 liverworts (8%) and 33 mosses (92%). In other words, the liverworts are very well represented in the soil surface of the acidophytic beech forests, but are almost insignificant in the diaspore bank. This evidence, together with the fact that most of them are colonists, leads us to

suppose that the liverworts must play an important role in this kind of forest when recovery after a disturbance begins, for instance developing a thin carpet which may prevent the soil from erosion or help to retain water and keep it wet. In fact, we think that this can be also applied to other acidophytic woods in other contexts, as has been proven to occur, after controlled fires, in an oak forest of *Quercus robur* belonging to the acidophytic association *Hyperico pulchri-Quercetum roboris* Rivas-Martínez, Bascónes, T.E. Díaz, Fernández-Gonzalez & Loidi 1991 (Urdíroz Ariz & Ederra Indurain, 1996), where several liverwort species appeared in the recovery process very soon.

On the other hand, the scarcity of liverworts in the diaspore bank, and their abundance in the soil surface, may also mean that many liverworts must have severe difficulties in producing long, medium or even short-life diaspores. Of course, liverworts produce spores and/or asexual propagules as mosses; there are evidences of dormancy, germinability, colonization efficiency, dispersal capacity and short or long periods of survival in some species as, for instance, *Lunularia cruciata* (L.) Dum., *Lophozia silvicola* Buch, and *Mannia fragans* (Balb.) Frye & L. Clark (Valio & Schwabe, 1969; Laaka-Lindberg, 1999; Laaka-Lindberg *et al.*, 2003; Hock *et al.*, 2008). Why, then, do liverworts tend to be rarer in the diaspore bank than in the above-ground vegetation? Van Zanten & Pocs (1981) and During (*in litt.*) pointed out that spores and asexual propagules of liverworts are relatively short-lived, intolerant of desiccation and unable to tolerate long periods of darkness. These could be reasons for the scarcity of hepatics in diaspore banks, but more studies are necessary to achieve greater knowledge and evidence to prove this.

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## REFERENCES

- BENSCOTER B.W., 2006 — Post-fire bryophyte establishment in a continental bog. *Journal of vegetation science* 17: 647-652.
- BIGGS L. & WITTKUHN R.S., 2006 — Bryophyte diaspore banks in soil and litter of an urban bushland in Perth, Western Australia. *Hikobia* 14(4): 375-382.
- BISANG I., 1996 — Quantitative analysis of the diaspore banks of bryophytes and ferns in cultivated fields in Switzerland. *Lindbergia* 21: 9-20.
- BISANG I., PIIPPO S. & HEDENÄS L., 2003 — Bryophyte diaspore bank in three Malaysian mountain rainforests. *Journal of bryology* 25: 68-70.
- BRAUN-BLANQUET J., 1979 — *Fitosociología*. Madrid, H. Blume Ediciones, 820 pp.
- CAILLIAU A. & PRICE M.J., 2007 — Hornworts in the agricultural fields of Genova: new findings, the soil diaspore bank and ex situ soil cultures. *Candollea* 62(2): 165-172.
- CANERS R.T., MACDONALD S.E. & BELLAND R.J., 2009 — Recolonization potential of bryophyte diaspore banks in harvested boreal mixed-wood forest. *Plant ecology* 204: 55-68.
- CLYMO R.S. & DUCKETT J.G., 1986 — Regeneration of *Sphagnum*. *New phytologist* 102: 589-614.
- DELGADO V. & EDERRA A., 2010 — Actualización de la brioflora de los hayedos de Navarra (Norte de España): especies características y variables determinantes. *Boletín de la sociedad Española de briología* 34/35: 1-17.
- DELGADO V. & EDERRA A., 2013 — Long-term changes (1982-2010) in the bryodiversity of Spanish beech forests assessed by means of Ellenberg indicator values of temperature, nitrogen, light and pH. *Biological conservation* 157: 99-107.
- DIERBEN K., 2001 — Distribution, ecological amplitude and phytosociological characterization of European bryophytes. *Bryophytorum bibliotheca* 56: 1-289.
- DURING H.J. & TER HORST B., 1983 — The diaspore bank of bryophytes and ferns in chalk grassland. *Lindbergia* 9: 57-64.

- DURING H.J., BRUGUÉS M., CROS R.M. & LLORET F., 1987 — The diaspore bank of bryophytes and ferns in the soil in some contrasting habitats around Barcelona. *Lindbergia* 13: 137-149.
- DURING H.J., 1992 — Ecological classifications of bryophytes and lichens. In: Bates J.W. & Farmer A.M. (eds.), *Bryophytes and lichens in a changing environment*. Oxford, Clarendon Press, pp. 1-31.
- DURING H.J., 1997 — Bryophyte diaspore banks. *Advances in bryology* 6: 103-134.
- DURING H.J. & MOYO C., 1999 — The diaspore bank of bryophytes in a Zimbabwean savanna. *Haussknechtia* 9: 111-114.
- DURING H.J., 2001 — New frontiers in bryology and lichenology – Diaspore banks. *The bryologist* 104: 92-97.
- DURING H.J., 2007 — Episodic bryophytes in the diaspore bank of a Zimbabwean savanna. *Lindbergia* 32: 55-61.
- DYER A.F. & LINDSAY S., 1992 — Soil spore banks of temperate ferns. *American fern journal* 82(3): 89-122.
- ECKSTEIN J., 2006 — Die Moosdiasporenbanken einiger Teichen im Ostthüringer Bundsandssteingebiet. *Herzogia* 19: 341-351.
- EDERRA A., IGLESIAS N., JUARISTI R. & HUARTE B., 2012 — Novedades para el catálogo briológico de Navarra (norte de España). *Botanica complutensis* 36: 35-38.
- ESSL F., STEINBAUER K., DULLINGER S., MANG T. & MOSER D., 2013 — Telling a different story: a global assessment of bryophyte invasions. *Biological invasions* 15: 1933-1946.
- FRAHM J.-P., 2012 — The phytogeography of European bryophytes. *Botanica Serbica* 36: 23-36.
- FREY W. & KÜRSCHNER H., 2011 — Asexual reproduction, habitat colonization and habitat maintenance in bryophytes. *Flora* 206(3): 173-184.
- FURNESS S.B. & HALL R.H., 1981 — An explanation of the intermittent occurrence of *Physcomitrium sphaericum* (Hedw.) Brid. *Journal of bryology* 11: 733-744.
- GHORBANI J., DAS P.M., DAS A.B., HUGHES J.M., McALLISTER H.A., PALLAI S.K., PAKEMAN R.J., MARRS R.H. & LEDUC M.G., 2003 — Effects of restoration treatments on the diaspore bank under dense *Pteridium* stands in the UK. *Applied vegetation science* 6: 189-198.
- GOBIERNO DE NAVARRA, 2014a — Mapa de vegetación potencial de Navarra. [http://www.cfnavarra.es/agricultura/informacion\\_agraria/mapaCultivos/htm/mapa.htm](http://www.cfnavarra.es/agricultura/informacion_agraria/mapaCultivos/htm/mapa.htm). Accessed the 07/19/2014.
- GOBIERNO DE NAVARRA, 2014b — Espacios naturales protegidos. [http://www.navarra.es/home\\_es/Gobierno+de+Navarra/Organigrama/Los+departamentos/Desarrollo+Rural+Industria+Empleo+y+Medio+Ambiente/Publicaciones/Publicaciones+propias/Publicaciones+medio+ambiente/Otros/#header2](http://www.navarra.es/home_es/Gobierno+de+Navarra/Organigrama/Los+departamentos/Desarrollo+Rural+Industria+Empleo+y+Medio+Ambiente/Publicaciones/Publicaciones+propias/Publicaciones+medio+ambiente/Otros/#header2). Accessed the 03/09/2014.
- HAMMER Ø., HARPER D.A.T. & RYAN P.D., 2001 — PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia electronica* 4(1): 9 pp.
- HASSEL K. & SÖDERSTRÖM L., 2005 — The expansion of the alien mosses *Orthodontium lineare* and *Campylopus introflexus* in Britain and continental Europe. *Journal of the Hattori botanical laboratory* 97: 183-193.
- HÉBRARD J.-P., 2001 — La banquet édaphique de diaspores de bryophytes de l'écosystème du chêne vert au bois d'Astros (commune de Vidauban, Var, France). *Nova Hedwigia* 73: 323-337.
- HOCK Z., SZÖVÉNYI P. & TÓTH Z., 2006 — Seasonal variation in the spore bank of ferns in grasslands on dolomite rock. *Plant ecology* 187: 289-296.
- HOCK Z., SZÖVÉNYI P., SCHNELLER J.J., TÓTH Z. & URMI E., 2008 — Bryophyte diaspore bank: a genetic memory? Genetic structure and genetic diversity of surface populations and diaspore bank in the liverwort *Mannia fragans* (Aytoniaceae). *American journal of botany* 95(5): 542-548.
- IGLESIAS TEIXEIRA N., 2013 — Estudio del banco de diásporas de briofitos de los hayedos de Navarra: biodiversidad, influencia de la profundidad y de la estacionalidad y dormancia. Tesis Doctoral. Navarra, Universidad de Navarra. <http://hdl.handle.net/10171/35129>.
- JONSSON B.G., 1993 — The bryophyte diaspore bank and its role after small-scale disturbance in a boreal forest. *Journal of vegetation science* 4: 819-826.
- LAAKA-LINDBERG S., 1999 — Asexual reproduction in a population of a leafy hepatic species *Lophozia silvicola* Buch in central Norway. *Plant ecology* 141: 137-144.
- LAAKA-LINDBERG S., KORPELAINEN H. & POHJAMO A., 2003 — Dispersal of asexual propagules in bryophytes. *Journal of the Hattori botanical laboratory* 93: 319-330.
- LA FARGE C., WILLIAMS K.H. & ENGLAND J.H., 2013 — Regeneration of Little Ice Age bryophytes emerging from a polar glacier with implications of totipotency in extreme environments. *Proceedings of the national academy of sciences of the United States of America* 110(24): 9839-9844.

- MACIEL-SILVA A.S., VALIO I.F. & RYDIN H., 2012 — Diaspore bank of bryophytes in tropical rain forests: the importance of breeding system, phylum and microhabitat. *Oecologia* 168: 321-333.
- MARGALEF R., 1986 — *Ecología*. Barcelona, Ediciones Omega, S.A., 951 pp.
- MARSHALL W.A. & CONVEY P., 1997 — Dispersal of moss propagules on Signy Island, maritime Antarctic. *Polar biology* 18: 376-383.
- MILLER N.G. & McDANIEL S.F., 2004 — Bryophyte dispersal inferred from colonization of an introduced substratum on Whiteface Mountain, New York. *American journal of botany* 91: 1173-1182.
- MUÑOZ J., FELICÍSIMO A.M., CABEZAS F., BURGAZ A.R. & MARTÍNEZ I., 2004 — Wind as a long-distance dispersal vehicle in the Southern Hemisphere. *Science* 304: 1144-1147.
- ORDÓÑEZ A., GUERRA J. & CANO M.J., 2003 — The bryophyte diaspore bank in soils affected by the Aznalcóllar (Seville, SW Spain) mine disaster. *Anales de biología* 25: 37-48.
- PAULIUK F., MÜLLER J. & HEINKEN T., 2011 — Bryophyte dispersal by sheep on dry grassland. *Nova Hedwigia* 92: 327-341.
- PIUDO M.J. & CAVERO R.Y., 2005 — Banco de semillas: Comparación de metodologías de extracción, de densidad y de profundidad de muestreo. *Publicaciones de biología de la Universidad de Navarra, serie Botánica* 16: 71-82.
- RIVAS-MARTÍNEZ S., FERNÁNDEZ-GONZÁLEZ F., LOIDI J., LOUSÁ M. & PENAS A., 2001 — Syntaxonomical checklist of vascular plant communities of Spain and Portugal to association level. *Itinera geobotanica* 14: 5-341.
- ROS R.M., MAZIMPAKA V., ABOU-SALAMA U., ALEFFI M., BLOCCKEEL T.L., BRUGUÉS M., CANO M.J., CROS R.M., DIA M.G., DIRKSE G.M., EL SAADAWI W., ERDAĞ A., GANEVA A., GONZÁLEZ-MANCEBO J.M., HERRNSTADT I., KHALIL K., KÜRSCHNER H., LANFRANCO E., LOSADA-LIMA A., REFAI M.S., RODRÍGUEZ-NUÑEZ S., SABOVLJEVIĆ M., SÉRGIO C., SHABBARA H., SIM-SIM M. & SÖDERSTRÖM L., 2007 — Hepatics and Anthocerotales of the Mediterranean, an annotated checklist. *Cryptogamie, Bryologie* 28: 351-437.
- ROS R.M., MAZIMPAKA V., ABOU-SALAMA U., ALEFFI M., BLOCCKEEL T.L., BRUGUÉS M., CROS R.M., DIA M.G., DIRKSE G.M., DRAPER I., EL SAADAWI W., ERDAĞ A., GANEVA A., GABRIEL R., GONZÁLEZ-MANCEBO J.M., GRANGER C., HERRNSTADT I., HUGONNOT V., KHALIL K., KÜRSCHNER H., LOSADA-LIMA A., LUIS L., MIFSUD S., PRIVITERA M., PUGLISI M., SABOVLJEVIĆ M., SÉRGIO C., SHABBARA H., SIM-SIM M., SOTIAUX A., TACCHI R., VANDERPOORTEN A. & WERNER O., 2013 — Mosses of the Mediterranean, an annotated checklist. *Cryptogamie, Bryologie* 34: 99-283.
- ROSS-DAVIS A.L. & FREGO K.A., 2004 — Propagule sources of forest floor bryophytes: spatiotemporal compositional patterns. *The bryologist* 107(1): 88-97.
- RYDGREN K. & HESTMARK G., 1997 — The soil propagule bank in a boreal old-growth spruce forest: changes with depth and relationship to aboveground vegetation. *Canadian journal of botany* 75: 121-128.
- SHIELDS J.A., WEBSTER C.R. & GLIME J.A., 2007 — Bryophyte community response to silvicultural opening size in a managed northern hardwood forest. *Forest ecology and management* 252: 222-229.
- SMITH R.I.L., 1987 — The bryophyte propagule bank of Antarctic fellfield soils. *Symposia biologica Hungarica* 35: 233-245.
- SMITH R.J., 2013 — Cryptic diversity in bryophyte soil-banks along a desert elevational gradient. *Lindbergia* 36: 1-8.
- TER BRAAK C.J.F. & ŠMILAUER P., 2002 — *CANOCO Reference manual and CanoDraw for Windows User's guide: Software for Canonical Community Ordination (version 4.5)*. Ithaca, Microcomputer Power, 500 pp.
- THOMPSON K., BAKKER J. & BEKKER R., 1997 — *The soil seed banks of North West Europe: methodology, density and longevity*. Cambridge, Cambridge University Press, 276 pp.
- URDÍROZ ÁRIZ A. & EDERRA INDURAIN A., 1996 — Estudio del impacto causado por los incendios en la brioflora de un robledal de Navarra (España). *Cryptogamie, Bryologie Lichénologie* 17(2): 135-142.
- VALIO I.F.M. & SCHWABE W.W., 1969 — Growth and dormancy in *Lunularia cruciata* (L.) Dum.: IV. Light and temperature control of rhizoid formation in gemmae. *Journal of experimental botany* 20(3): 615-628.
- VAN ZANTEN B.O. & POCS T., 1981 — Distribution and dispersal of bryophytes. *Advances in bryology* 1: 479-562.
- ZANDER R.H. & DURING H.J., 1999 — *Neophoenix (Pottiaceae)*, a new African moss found through soil diaspore bank analysis. *Taxon* 48: 657-662.