RELEVANCE OF BROAD-LEAVED FOREST STANDS FOR MAINTAINING EPIPHYTIC BRYOPHYTE SPECIES AND FUNCTIONAL TRAIT DIVERSITY IN FOREST LANDSCAPE IN LATVIA

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Broad-leaved trees play an important role in supporting epiphyte richness in deciduous forests. In this study we tested which broad-leaved forest stands in terms of tree composition best predicted biodiversity in regard to bryophyte species number and their functional traits. The bryoflora was surveyed in 70 stands differing in dominant broad-leaved tree species. One circular plot with diameter 30 meters was established in each stand situated in different parts of Latvia. Fifty-three of the plots were located in stands identified as protected habitats of the European Union. In total, 82 bryophyte species were recorded. At plot level the total number of species ranged between 6 and 38 species. Using principal component analysis (PCA), the ordination axes explained 41% of the variation in composition of bryophytes. The PCA axes were related to tree species composition. The presence of broad-leaved trees, especially ash, lime, and oak, was connected with higher species richness. Generalised linear models confirmed that epiphyte richness, both at the total and indicator species levels, was higher in ash stands. From the functional traits, all expected life-strategy and life-form categories were recorded. The most represented life-forms were smooth mats, tall turfs, and rough mats, while the dominant life-strategy was perennial stayers, followed by competitive perennials and long-lived shuttles. Functional trait richness was highest in Fraxinus excelsior, Tilia cordata, and Quercus robur forest stands.

Key words: epiphytes, bryoflora, indicators, tree diversity, life-strategies, life-forms.

INTRODUCTION

Biological diversity in European forests has become one of the most important subjects in environmental policy (Convention on Biological Diversity, 2020), most likely because of dramatic changes in ecosystems over the last century (Bengtsson *et al.*, 2000). Although broad-leaved forests have been intensively managed in Europe (Dieler *et al.*, 2017), nowadays they still have an important role in conservation of cryptogams (Nordén *et al.*, 2007). Broad-leaved forests are associated with high epiphytic bryophyte species diversity in the boreal coniferous forest landscape (Löbel *et al.*, 2006; Dittrich *et al.*, 2016). The epiphytic species composition and richness in these forests are influenced by various environmental factors. Some of the most significant characteristics are the host tree species and tree size, as well

as forest stand quality (Király *et al.*, 2013). In the boreal forest zone, broad-leaved tree species, especially maple and ash, have been associated with the highest epiphytic bryophyte diversity (Snäll *et al.*, 2004; Löhmus *et al.*, 2007).

Studies of species functional traits like life-strategies or life-forms in Latvia (Strazdiņa *et al.*, 2013; Mežaka and Kirillova, 2019; Ievinsh *et al.*, 2020) and in other countries from the boreal region (Darell and Cronberg, 2011; Michel *et al.*, 2012) have shown that there is different specificity to host tree characteristics and habitat conditions. Some species, especially rare species and indicators of pristine forests, are dependent on large areas of long forest continuity with specific niche abundance (Hedderston, 1992; Söderström, 2006). These species are mostly represented by life-

forms with complex architecture such as tails, tall turfs, mats, and wefts (Mägdefrau, 1969) and life-strategies such as long-lived shuttles or perennial stayers with limited sporophyte production (During, 1992; Kürschner, 2004). At the same time, other species require only small unmanaged patches or even single trees in managed forest landscapes where they can easily propagate and disperse to the next available niche. Examples of these species represent compact, desiccation tolerant small cushion, short turf and weft life-forms with colonist or pioneer life-strategy properties to produce many spores (Friedel *et al.*, 2006; Patiño *et al.*, 2009; Sporn *et al.*, 2010). These patterns have been explained by bryophyte physiology and adaptation to the four most important factors affecting their growth: light, moisture, substrate, and inter-species relations that are directly linked to bryophyte distribution rates (Bates, 1998; Virtanen, 2014).

There is a need to survey diversity of species in forest ecosystems. Therefore, the aim of this study was, firstly, to determine the epiphytic bryophyte species richness and composition in broad-leaved forests of Latvia, and, secondly, to examine the epiphyte functional trait composition and diversity in broad-leaved forests.

MATERIALS AND METHODS

Study area. The research area covered the whole territory of Latvia (Fig. 1). Latvia is located in the northern part of Europe in the boreo-nemoral vegetation zone (Sjörs, 1963). The mean annual temperature varies from 4.9 °C to 7.1 °C and the mean annual precipitation is from 576 mm to 757 mm (Avotniece *et al.*, 2017). The greater part of the forest area is dominated by coniferous trees Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*. The forests of noble broad-leaved trees occupy only one per cent of the forest area in Latvia (Meža nozare..., 2020).

Field sampling. In total, 70 stands were randomly selected, which ensured representative sampling of eight target tree species in the common noble broad-leaved forest types in Latvia. The studied stands were dominated by different noble broad-leaved tree species — European ash *Fraxinus excelsior* (18 stands), pedunculate oak *Quercus robur* (16), small-leaved lime *Tilia cordata* (11), Norway maple *Acer platanoides* (9), common hornbeam *Carpinus betulus* (4), common beech *Fagus sylvatica* (2), and mixed European white elm *Ulmus laevis* and wych elm *Ulmus glabra* forests (10). The age of stands varied from 20 years (maple) to 206 years (oak). The stands represented *Aegopodiosa* (32 stands), *Oxalidosa* (17), *Hylocomiosa* (12), *Oxalidosa turf. mel.* (4), *Filipendulosa* (2), *Dryopteriosa* (1), *Myrtillosa mel.* (1) and *Mercurialiosa mel.* (1) forest site types. The majority of studied stands were located on mineral soils (62 stands), four on drained peat soils, two on peat soils, one on wet mineral soils and one on drained mineral soils.

The data were collected during five summer seasons from 2015 to 2019. One circular plot (D = 30 m) was established

Fig. 1. Location of the studied forest stands in Latvia (plots are marked with black dots).

at randomly chosen coordinates in each of the selected stands. In each plot, five randomly chosen living trees from each tree species were described, recording all bryophyte species found from tree base up to 2 m height and determining the percentage cover of each epiphyte species. Unknown species were collected and later identified in the laboratory. Nomenclature followed Āboliņa *et al.* (2015). In some plots the minimum number of trees was lacking, and therefore the total number of studied trees was not always constant.

Data analysis. Generalised linear models (GLM) were applied to assess the differences in mean species richness (number of species) per tree among the studied forest stands dominated by different broad-leaved trees (stands of: (1) *Tilia cordata*, (2) *Quercus robur* (used as intercept), (3) *Fraxinus excelsior*, (4) *Carpinus betulus*, (5) *Acer platanoides*, (6) mixed *Ulmus laevis* and *Ulmus glabra* stands and (7) *Fagus sylvatica* stands). The Poisson residual distribution and log link were used. To assess the differences in species composition and functional trait diversity in relation to major forest stand variables, we applied principal components analysis (PCA) and indicator species analysis of plots (n = 70) (Peck, 2010). The species abundance data were used in the ordination as the species matrix and environmental variables (stand age, forest stand status as EU protected habitat, number of broad-leaved tree species, number of deciduous tree species, bryophyte species richness, number of indicators, life-form richness, life-strategy richness) as the environmental matrix. PCA and Indicator Species Analysis were done in PC-ORD 6 (Peck, 2010), other analyses were performed in R v. 3.1.2 (A language and..., 2017).

RESULTS

Species richness. In total, we recorded 82 bryophyte species on the studied trees (Table 1). Epiphytic bryophytes were determined on 19 tree species. Mosses (68 species, 83%) contributed to the majority of species richness while liverworts were represented in much lower numbers (14 species, 17%). Among the recorded bryophytes, 14

Table 1. Recorded 82 bryophyte species on studied trees (n = 1034) and in the studied plots (n = 70). Bryophyte species trait classification was based on literature: life-forms after Bates (1998), life-strategies after During (1979; 1992), growth forms, gametophyte types, fruiting frequency, fruiting seasons after Bernhardt-Römermann *et al.* (2018).

Bryophyte species	In studied stands	On studied trees	In studied plots	Life-form	Life-strategy	Growth form	Gametophyte type	Fruiting frequency	Fruiting season
<i>Abietinella abietina</i>	U	2	2	W	p	P	D	vr	sp
<i>Amblystegium serpens</i>	all	254	47	Mr	p	P	M	c	sp to a
<i>Amblystegium subtile</i>	TFA	146	27	Ms	p	P	M	c	su to a
<i>Amblystegium varium</i>	TQFA	66	22	Ms	p	P	M	o	sp
<i>Anomodon attenuatus*</i>	FU	4	2	Ta	p	P	D	vr	a
<i>Anomodon longifolius*</i>	TQFCAU	47	15	Ta	p	P	D	vr	a to w
<i>Anomodon viticulosus*</i>	QFCU	22	8	Ta	p	P	D	r	w
<i>Atrichum undulatum</i>	QFC	3	3	Te	s	O	M	c	w
<i>Blepharostoma trichophyllum</i>	TQF	3	3	Mt	c	P	M	o to f	sp to su
<i>Brachytheciastrum velutinum</i>	TQFCU	34	15	Mr	p	P	M	f	w to sp
<i>Brachythecium campestre</i>	F	2	1	Mr	p	P	M		a to w
<i>Brachythecium glareosum</i>	Q	2	2	Te	p	P	D	rare	w
<i>Brachythecium mildeanum</i>	U	1	1	Mr	p	P	M		
<i>Brachythecium plumosum</i>	F	1	1	Te	p	P	M	f	w
<i>Brachythecium rutabulum</i>	all	384	60	Mr	cp	P	M	c	a to sp
<i>Brachythecium salebrosum</i>	TQFA	77	27	Mr	p	P	M	o	a to w
<i>Bryum capillare</i>	T	1	1	CU	c	O	D	c	sp to su
<i>Bryum moravicum</i>	TQA	4	4	CU	c	O	D	c	
<i>Calliergonella cuspidata</i>	F	2	2	W	pc	P	D	o	sp
<i>Calypogeia sp.</i>	TQ	2	2	Ms	c	P	D, M	c	sp
<i>Cephalozia bicuspidata</i>	Q	2	1	Mt	cp	P	M	c	a to sp
<i>Cephaloziella sp.</i>	Q	1	1	t	c	P	D	r	sp to su
<i>Chiloscyphus pallescens</i>	TQFA	8	6	Mt	pc	P	M	r to o	w to sp
<i>Cirriphyllum piliferum</i>	TQFUS	31	17	Mt	pc	P	D	r	a to w
<i>Climacium dendroides</i>	QF	7	6	D	pc	O	D	vr	a to w
<i>Dicranum montanum</i>	all	206	48	t	pc	O	D	r	su
<i>Dicranum polysetum</i>	F	1	1	Te	pc	O	D	r	su to a
<i>Dicranum scoparium</i>	all	49	26	Te	cp	O	D	r	su to w
<i>Eurhynchium angustirete</i>	FCAS	101	21	Mr	p	P	D	r to o	a to w
<i>Eurhynchium striatum</i>	TQF	69	14	Mr	p	P	D	r to o	a to w
<i>Fissidens adianthoides</i>	F	8	4	Te	c	O	D, M	f	a to sp
<i>Fissidens taxifolius</i>	QF	2	2	Te	c	O	M	f	w to sp
<i>Frullania dilatata</i>	TQFCAS	76	20	Ms	l	P	D	f	a to sp
<i>Frullania fragilifolia</i>	F	8	2	t	l	P	D	r	sp to su
<i>Frullania tamarisci*</i>	FC	5	3	W	l	P	D	o	sp to a
<i>Herzogiella seligeri</i>	FU	2	2	Mr	ps	P	M	c	su
<i>Homalia trichomanoides*</i>	all	343	55	Ms	ps	P	M	o to f	w
<i>Homalothecium lutescens</i>	F	4	3	W	p	P	D	r	w
<i>Homalothecium sericeum</i>	TQFCUS	20	11	Ms	p	P	D	o	w
<i>Hylocomium splendens</i>	QF	6	3	W	pc	P	D	r	sp
<i>Hypnum cupressiforme</i>	all	597	64	Ms	ps	P	D	f	a
<i>Isoetecium alopecuroides*</i>	TQFCS	40	14	D	ps	P	D	o to f	a to w
<i>Isoetecium myosuroides*</i>	U	1	1	D	p	P	D	f to c	w
<i>Lejeunea cavifolia*</i>	TQF	24	11	t	l	P	M	o	su to w
<i>Lepidozia reptans</i>	F	1	1	Mt	cp	P	M	o	w to su
<i>Leskea polycarpa</i>	T	3	2	Mr	p	P	M	c	sp to su
<i>Leucodon sciurioides</i>	TQFCU	147	28	Ta	l	P	D	vr	w to sp
<i>Lophocolea heterophylla</i>	TQFAUS	52	26	Mt	cp	P	M	c	a to sp
<i>Metzgeria furcata*</i>	all	92	22	Ms	l	P	D	o	sp to w
<i>Mnium hornum</i>	QFU	8	8	Te	l	O	D	f	sp

Table 1. (Continued)

Bryophyte species	In studied stands	On studied trees	In studied plots	Life-form	Life-strategy	Growth form	Gametophyte type	Fruiting frequency	Fruiting season
<i>Neckera complanata</i> *	TFC	16	7	Ms	p	P	D	o	sp
<i>Neckera pennata</i> *	TQFAU	110	23	Ms	l	P	M	c	a to w
<i>Orthotrichum affine</i>	all	114	28	cu	c	O	M	c	sp to su
<i>Orthotrichum lyellii</i> *	F	1	1	t	s	O	D	r	su
<i>Orthotrichum speciosum</i>	QFCAUS	113	29	cu	s	O	M	c	w to sp
<i>Oxyrrhynchium hians</i>	TQFCAU	68	30	Ms	cp	P	D	r	w
<i>Plagiochila asplenoides</i>	TQF	40	12	Te	p	P	D	vr	sp to su
<i>Plagiomnium affine</i>	QFCAUS	26	13	Te	pc	O	D	vr	sp
<i>Plagiomnium cuspidatum</i>	TQFAU	157	37	Te	pc	O	M	f	sp to su
<i>Plagiomnium undulatum</i>	FCU	35	15	D	pc	O	M	r	sp
<i>Plagiothecium cavifolium</i>	F	6	4	Mr	ps	P	D	r	su
<i>Plagiothecium denticulatum</i>	FA	4	2	Ms	ps	P	M	c	sp to su
<i>Plagiothecium latebricola</i> *	S	2	1	Ms	ps	P	D	r	w
<i>Plagiothecium laetum</i>	TQFAS	65	22	Ms	ps	P	M	f	a
<i>Platygyrium repens</i>	TQFCA	75	28	Mr	ps	P	D	vr	w to sp
<i>Pleurozium schreberi</i>	TQF	7	4	W	pc	P	D	vr	a to w
<i>Pohlia nutans</i>	F	1	1	t	cp	O	M	f	sp to su
<i>Pseudobryum cinclidioides</i>	T	1	1	Te	l	O	D	vr	su
<i>Pseudoleskella nervosa</i>	A	1	1	Te	p	P	D		su
<i>Ptilidium pulcherrimum</i>	QFA	13	8	Ms	s	P	D	o	su
<i>Pylaisia polyantha</i>	TQFAUS	179	45	Mr	p	P	M	c	a to w
<i>Radula complanata</i>	all	618	66	Ms	l	P	M	c	sp to w
<i>Rhizomnium punctatum</i>	QF	4	4	Te	l	O	D	f	a to w
<i>Rhodobryum roseum</i>	TF	3	3	Te	c	O	D	vr	a
<i>Rhytidiadelphus triquetrus</i>	TF	7	4	W	pc	P	D	r	w
<i>Sanionia uncinata</i>	FUS	6	4	Mr	ps	P	M	f to c	sp to su
<i>Sciuro-hypnum oedipodium</i>	F	9	6	Mr	pc	P	M	c	w
<i>Sciuro-hypnum populeum</i>	TQFC	26	14	Te	p	P	M	f	a to sp
<i>Tetraphis pellucida</i>	TFS	4	4	t	cp	O	M	r to o	sp to w
<i>Thuidium delicatulum</i>	TQF	19	8	W	p	P	D	o	w
<i>Thuidium tamariscinum</i>	FCU	17	10	W	p	P	D	r	w to sp
<i>Ulota crispa</i> *	all	112	38	cu	l	O	M	c	su

* rare, especially protected, red-listed or woodland key habitat indicator species. Forest stands: T, *Tilia cordata*; Q, *Quercus robur*; F, *Fraxinus excelsior*; C, *Carpinus betulus*; A, *Acer platanoides*; U, *Ulmus* spp.; S, *Fagus sylvatica*. Life-form: cu, small cushion; CU, large cushion; D, dendroid; Mr, rough mat; Ms, smooth mat; Mt, thread-like mat; t, short turf; Ta, tail; Te, tall turf; Th, thalloid-mat; W, weft. Life-strategy: c, colonist; cp, pioneer; l, long-lived shuttle; p, perennial stayer; pc, competitive perennial; ps, stress-tolerant perennial; s, short lived shuttle. Growth form: P, plagiotropic; O, orthotropic. Gametophyte type: D, dioicous; M, monoicous. Fruiting frequency: c, common; o, occasional; f, frequent; r, rare; vr, very rare. Fruiting season: sp, spring; su, summer; a, autumn; w, winter.

epiphytic species were red-listed, rare, especially protected or used as woodland key habitat indicators in Latvia (Auniņš, 2013) — *Anomodon attenuatus*, *A. longifolius*, *A. viticulosus*, *Frullania tamarisci*, *Homalia trichomanoides*, *Isothecium alopecuroides*, *I. myosuroides*, *Lejeunea cavifolia*, *Metzgeria furcata*, *Neckera complanata*, *N. pennata*, *Orthotrichum leyellii*, *Plagiothecium latebricola*, and *Ulota crispa*. These species were referred to as woodland key habitats (WKH) indicators further in the text.

The ten most common species found in all seven forest stand types were: *Amblystegium serpens*, *Brachythecium rutabulum*, *Dicranum montanum*, *Dicranum scoparium*, *Hypnum cupressiforme*, *Orthotrichum affine*, *Radula*

complanata, and also three indicators *Homalia trichomanoides*, *Metzgeria furcata*, and *Ulota crispa*. The twelve least common species that were found only in one of 70 plots were *Brachythecium campestre*, *Brachythecium mildeanum*, *Brachythecium plumosum*, *Bryum capillare*, *Cephalozia* sp., *Cephaloziella* sp., *Dicranum polysetum*, *Lepidozia reptans*, *Orthotrichum lyellii*, *Plagiothecium latebricola*, *Pohlia nutans*, and *Pseudobryum cinclidioides*.

The total number of species was found to be much higher in the studied *Fraxinus excelsior* stands (Fig. 2). In addition, the mean number of total epiphytic species per studied plot was greater in the *Fraxinus excelsior* and *Tilia cordata* stands (Table 2). Twelve WKH indicators were found on

Fig. 2. Total bryophyte species, life-form and life-strategy richness in studied forest stands. Number of woodland key habitats (WKH) indicators for each variable was added on the bars.

Table 2. Mean number of bryophyte species in different forest stands with different dominant tree species. The *p* value indicates differences between reference and other levels, using generalised linear model (GLM) analysis

Studied forest stands	Number of studied forest stands	Mean number of epiphytic species per studied plot $\pm$ Std. error	<i>p</i> value
All bryophyte species			
<i>Quercus robur</i> (intercept)	16	13 $\pm$ 0.93	0.001
<i>Tilia cordata</i>	11	16 $\pm$ 1.98	0.001
<i>Fraxinus excelsior</i>	18	24 $\pm$ 1.57	0.001
<i>Carpinus betulus</i>	4	14 $\pm$ 1.03	0.1
<i>Fagus sylvatica</i>	2	16 $\pm$ 1.5	0.05
<i>Acer platanoides</i>	9	14 $\pm$ 1.19	
<i>Ulmus laevis</i> , <i>Ulmus glabra</i>	10	11 $\pm$ 0.91	
Woodland key habitats (WKH) indicators			
<i>Quercus robur</i> (intercept)	16	2 $\pm$ 0.30	0.001
<i>Tilia cordata</i>	11	3 $\pm$ 0.71	0.001
<i>Fraxinus excelsior</i>	18	4 $\pm$ 0.57	0.001
<i>Carpinus betulus</i>	4	5 $\pm$ 0.70	0.001
<i>Fagus sylvatica</i>	2	3 $\pm$ 2	0.1
<i>Acer platanoides</i>	9	2 $\pm$ 0.35	
<i>Ulmus laevis</i> , <i>Ulmus glabra</i>	10	2 $\pm$ 0.54	

the trees in ash stands, comprising the highest number of epiphytic indicators among all studied stands. Together with *Carpinus betulus* and *Tilia cordata* stands, these three forests were characterised by the highest richness of epiphytic WKH indicators. The number of species was related to different forest stands, as significant differences ($p < 0.05$) between stands with different dominant broad-leaved trees were revealed by GLM analysis.

Bryophyte functional traits. In total, bryophytes represented ten different life-forms, of which smooth mats (16 species), tall turfs (16), and rough mats (15) were the most common. This tendency was true also for the indicator species; half of all indicators had a smooth mat or tall turf life-form. The highest life-form richness was recorded in *Fraxinus excelsior* stands, followed by *Tilia cordata* and *Quercus robur* stands (Figs. 2, 3). The cushion form was the least characteristic in the studied forests; the large cushion form was represented only by two species and the small cushion by three species.

Fig. 3. Life-form richness in different studied forest stands with species number shown in parentheses. Number of WKH indicators representing corresponding life-forms is also given.

Fig. 4. Life-strategy richness in different studied forest stands with species numbers shown in parentheses. Number of WKH indicators representing corresponding life-forms is also given.

The recorded bryophyte species represented seven life-strategies. The most common strategy with 26 species was perennial stayer, followed by competitive perennials (13 species) and long-lived shuttles (12). Indicators corresponded to four different strategies, from them the long-lived shuttles and perennial stayers were the most common, both represented by five species. Similar to previously described trends, the highest life-strategy richness was recorded in *Fraxinus excelsior* stands, as well as in *Tilia cordata* and *Quercus robur* stands (Figs. 2, 4).

Analysing other bryophyte traits (Table 1), species composition could be divided according to growth form, where the plagiotropic species significantly dominated over oligotrophic species, i.e. 60 to 22, respectively. Two species groups of similar size were classified depending on gametophyte propagation properties — 35 monoicous and 45 dioicous species, plus two species representing both types. Five categories were divided according to fruiting frequency, from which dominated species with common (19 species) or rare (17) development of fruits. Regarding the fruiting season, 13 different types were found. The most common fruiting time in the studied forest stands was winter (13 species), followed by a longer period from autumn to winter (12), and period from spring to summer (11).

Principal component analysis and indicator species analysis. The PCA biplot of bryophyte species composition is shown in Figure 5. Total variance explained by the first pair of axes was 41%. The studied forest plots grouped along axes PC1 and PC2 in the ordination according to bryophyte species composition and dominant tree species in the plot. Negative correlation (Pearson coefficient $r < -0.6$) was found between all biodiversity variables and PC1, except

Fig. 5. Principal component analysis of broad-leaved forest stand plots ($n = 70$) based on abundance data of epiphytic bryophyte species (82 species). Colour of plot symbol shows if it was identified as protected forest habitat of European Union (filled) or not (empty). Clusters of the most influential forest stand plots are marked as follows: *Fraxinus excelsior* plots (I), joint *Tilia cordata* and *Quercus robur* plots (II), mixed *Ulmus laevis* and *Ulmus glabra* plots (III), *Acer platanoides* plots (IV). Eigenvalues of axes: PC1 = 0.459, PC2 = 0.299. Explained variation was 41%; $p < 0.001$. Meaning of numbers on vectors and Pearson correlation is given in Table 3.

for the forest age (Table 3). Four distinct clusters of forest plots were recognised, each of which had an indicator species listed in Table 4. *Fraxinus excelsior* stands (cluster I) tended to have the highest number of species, including WKH indicators. Bryophyte species like *Frullania fragilifolia*, *Homalothecium lutescens*, *Lepidozia reptans*, *Orthotrichum lyellii*, and *Plagiothecium cavifolium* etc. were found only in ash plots. However, no species showed statistically significant relation with *Fraxinus excelsior* stands (Table 4). *Tilia cordata* and *Quercus robur* stand plots formed a joint cluster (cluster II) sharing similar species composition between themselves and partly overlapping also with *Fraxinus excelsior* stand plots. Examples of species that were common only in all three of these forest stands were *Amblystegium varium*, *Blepharostoma trichophyllum*, *Brachythecium salebrosum*, *Eurhynchium striatum*, *Lejeunea cavifolia*, *Plagiochila asplenioides*, and *Thuidium delicatulum*. Five species were significantly associated to lime and oak stands. Cluster III belonged to mixed *Ulmus laevis* and *U. glabra* stand plots and was associated with species like *Abietinella abietina*, *Brachythecium mildeanum*, *Herzogiella seligeri*, and *Isothecium myosuroides*. From all species, only *Amblystegium serpens* was significantly related to *Ulmus* spp. stands. Cluster IV was formed by *Acer platanoides* plots, which mostly overlapped with bryophyte communities of the other studied forest stand types. Three species (*Amblystegium subtile*, *Orthotrichum speciosum*, and *Pylaisia polyantha*) were significantly associated to maple stands. According to Indicator Species Analysis, the largest number of indicators was found in the two studied *Fagus sylvatica* stands (Table 4). Richness of bryophyte species, WKH indicators and functional traits showed positive relationship with stands that

Table 3. Pearson correlations between forest stands, bryophyte species richness and bryophyte functional traits with principal component analysis axes 1 and 2. Used variables 1–6 are shown as numbered vectors in Figure 5.

Group	PC1	PC2
1. No of broad-leaved tree species	−0.647	−0.145
2. No of deciduous tree species	−0.605	0.01
3. Bryophyte species richness	−0.663	0.4
4. No of WKH indicators	−0.63	0.154
5. Age of forest stand	0.045	0.002
6. Life-form richness	−0.459	0.271
7. Life-strategy richness	−0.263	0.041
Life-form		
Smooth mat	−0.621	0.316
Tall turf	−0.427	0.507
Rough mat	−0.497	0.262
Weft	−0.249	0.3
Short turf	−0.419	0.437
Thread-like mat	−0.346	0.36
Tail	−0.404	−0.298
Dendroid	−0.203	0.233
Small cushion	−0.157	−0.137
Large cushion	0.032	−0.007
Life-strategy		
Perennial stayer	−0.652	0.128
Competitive perennial	−0.374	0.496
Long-lived shuttle	−0.562	0.27
Stress-tolerant perennial	−0.401	0.478
Colonist	0.005	−0.096
Pioneer	−0.325	0.319
Short lived shuttle	−0.167	0.083

Table 4. Statistically significant indicator bryophyte species for different forest stand types identified using indicator species analysis

Studied forest stands	Bryophyte species	p value
<i>Tilia cordata</i>	<i>Eurhynchium striatum</i>	0.025
<i>Quercus robur</i>	<i>Brachythecium salebrosum</i>	0.009
	<i>Eurhynchium angustirete</i>	0.044
	<i>Plagiomnium undulatum</i>	0.021
	<i>Sciuro-hypnum oedipodium</i>	0.045
<i>Carpinus betulus</i>	<i>Isothecium alopecuroides</i>	0.021
<i>Acer platanoides</i>	<i>Amblystegium subtile</i>	0.019
	<i>Orthotrichum speciosum</i>	0.057
	<i>Pylaisia polyantha</i>	0.03
<i>Ulmus laevis</i> , <i>Ulmus glabra</i>	<i>Amblystegium serpens</i>	0.043
<i>Fagus sylvatica</i>	<i>Cirriphyllum piliferum</i>	0.046
	<i>Lophocolea heterophylla</i>	0.046
	<i>Orthotrichum affine</i>	0.003
	<i>Plagiothecium latebricola</i>	0.026
	<i>Sanionia uncinata</i>	0.002
	<i>Tetraphis pellucida</i>	0.031
	<i>Ulotia crispa</i>	0.029

Fig. 6. Principal component analysis of bryophyte functional traits (10 life-forms, 7 life-strategies). Statistically significant correlations ($r \leq \pm 0.5$) between PCA ordination axes and bryophyte life-forms: smooth mat (a), tall turf (b), and life-strategies: long-lived shuttle (c), perennial stayer (d). Pearson correlation is given in Table 3.

had been identified as protected forest habitats of European Union.

PCA analysis was used to indicate differences in bryophyte functional trait categories in the studied forest stands. Pearson (r) correlations with the ordination axes were statistically significant only to two of the ten bryophyte life-forms (smooth mat with PC1; tall turf with PC2) and to two of seven life strategies (perennial stayers and long-lived shuttles with PC1) (Table 3, Fig. 6).

DISCUSSION

The diversity of epiphytic bryophytes was described in broad-leaved forests throughout the territory of Latvia. In our study the seven broad-leaved forest stand types, each with a different dominant tree species, were characterised with epiphyte richness similar to other published studies. For example, Mežaka *et al.* (2012) reported a total of 73 epiphytic bryophytes in deciduous woodland key habitats. The same number of bryophytes was found in a study by the author in deciduous forest stands in Latvia (Madžule *et al.*, 2012). The results showed that according to species composition, 17% of all recorded species were rare or protected, and 13% were indicators of woodland key habitats (Auniņš, 2013). Among them, six bryophyte species — *Isoetecium myosuroides*, *Lejeunea cavifolia*, *Neckera pennata*, *Neckera complanata*, *Orthotrichum lyellii*, *Plagiothecium latebricola* — are included in the Red Data Book of Latvia (Liepiņa, 2017). This may confirm the fact that most of the studied stands represented high-quality habitats with natural forest characteristics (Timonen *et al.*, 2010), which can explain why they were identified as protected habitats of European Union importance. Many authors have also shown that stands with dominating broad-leaved trees have high conservation value in the boreo-nemoral forest region (Ikaunieca *et al.*, 2012).

The highest number of all recorded species (85% from all listed bryophytes) and of WKH indicator species (86% from all recorded indicators) was found in ash stands, while the lowest number of total and WKH indicator species (28% and 35%, retrospectively) was recorded in beech stands. In addition, both the results of GLM analysis and PCA ordination indicated that *Fraxinus excelsior* forests were the species richest stands among all studied plots. We assume that this was due to a higher proportion of ash trees, which are associated with more suitable microhabitats for bryophytes. This is in accordance with the obtained results that the studied ash stands had higher number of rare and especially protected species. However, we did not analyse species composition at tree level. It is well known that of the broad-leaved tree species, European ash is an important substrate providing conditions for a large diversity of epiphytes (Mitchell *et al.*, 2014).

The studied ash stands were characterised with high diversity of different tree species (maximum was five deciduous tree species per studied *Fraxinus excelsior* plot). It has been shown in other studies that this factor correlates positively with the epiphytic species richness per stand (Lõhmus *et al.*, 2007; Király and Ódor, 2010).

We have to consider that in this survey it was difficult to compare the composition of bryophyte species between forest stand types because of high variability of different characteristics like age or tree layer structure of the studied plots. This also could explain why species composition of *Acer platanoides* stands was overlapping with bryophyte composition of almost all other studied forest stand types. Although maple is usually related with high species richness in forests, in our study the chosen maple stands represented different ages (from 20 to 124 years). The age variation may be the reason why the species found in maple stands were shared among all other forest types (dominated by the so called generalist species) and also explain the low number of epiphytes in maple plots in general. Additionally it could be related with a low number of deciduous tree species per plot (maximum three species) in the studied maple stands.

Usually a strong positive correlation is found between bryophyte richness and forest age, which is related with tree bark structure (due to increasing roughness with age), substrate longevity and continuity (Friedel *et al.*, 2006; Boudreault *et al.*, 2008; Fritz and Brunet, 2010). However, no correlation with forest age was found in our study. This could be explained by a very diverse tree species composition. All tree species can be arranged by age when they reach best suitability for epiphytes, although it is not always related with age per se. For example, ash and maple are overgrown by bryophytes already when young, as their bark acidity plays a more important role than tree age. However, even old oak and hornbeam trees are poor with epiphytes due to lack of scars on bark. Age might correlate with bryophyte richness within a tree species level but not if different species are compared.

It is also possible that bryophyte diversity was closely associated with the number of studied stands and trees (Łubek *et al.*, 2019), as some forest types were represented by more than ten plots while others only by less than five plots. However, the average species number per plot in mixed *Ulmus* spp. or in *Acer platanoides* stands was similar to species number recorded in *Quercus robur* stands (oak plots were twice as much represented). It may be that by increasing the number of study plots we would only slightly supplement the species records.

The studied forest stands provided high-quality conditions not only for the epiphyte diversity per se, but also their functional traits. Seven of all known eight life-strategies and ten of all known twelve life-forms were present in the studied plots. The lacking life-forms (thalloid mats characteristic of complex thalloid liverworts and sphagnoids or *Sphagnum* species) were missing only due to the fact that they are rarely epiphytic. The lacking life-strategy, fugitives, are generally non-existent in stable forest ecosystems. These results suggest a diverse niche abundance in the study sites.

Higher representation of species with more complex life-forms (such as smooth mat, rough mat, tall turf) and long-term life-strategies (like perennial stayer) are consistent with previous studies about bryophyte adaptation to moist microclimate and shadier conditions within unmanaged forest habitats (Strazdiņa *et al.*, 2013). *Fraxinus excelsior*, *Tilia cordata*, and *Quercus robur* forest stands provided more suitable environment for life-form and life-strategy richness than other stands, most probably due to more diverse tree layer structure and composition, presence of phorophytes of different size and age, as well as stand continuity. Other bryophyte functional traits beside life-strategies and life-forms also showed high diversity, stressing the importance of niches where species with different adaptations to spore distribution time or sporophyte position can coexist together, eliminating inter-species competition for the same resources (Li and Vitt, 1994; Cleavitt, 2002).

CONCLUSIONS

Our results showed that noble broad-leaved forest stands with high species richness of trees increases the opportunity of higher epiphytic bryophyte species diversity, especially of those species that are closely related to specific microhabitats. In this survey we showed that broad-leaved tree forests are diverse with regard also to bryophyte functional traits. In conclusion, we suggest to ensure the existence of deciduous tree forests with mixed broad-leaved tree species in managed forest landscapes to promote larger epiphyte species diversity. In cases when the broad-leaved forest stands are rich with WKH indicators and correspond to the status of EU forest habitat, we stress that their conservation and protection is crucially necessary to maintain the biological diversity in future.

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PLATLAPJU MEŽAUDŽU NOZĪME EPIFĪTISKO SŪNU SUGU UN TO FUNKCIONĀLO GRUPU DAUDZVEIDĪBAS VEICINĀŠANĀ LATVIJAS MEŽA AINAVĀ

Platlapju koku sugas veicina epifītu bagātību lapu koku mežos. Šajā pētījumā analizēts, kādu platlapju mežaudzes saistītas ar lielāku sūnu sugu un to funkcionālo grupu daudzveidību. Briofloras uzskaitē veikta visā Latvijas teritorijā mežaudzēs, kurās dominē septiņas dažādas platlapju koku sugas. Kopumā ierīkoti 70 apļveida parauglaukumi ($D = 30$ m). No visiem apsekotajiem parauglaukumiem 53 audzes atbilst kādam Eiropas Savienības nozīmes aizsargājamam mežu biotopam. Kopā konstatētas 82 sūnu sugas, to skaits parauglaukumos variēja no 6 līdz 38 sugām. Galvenajā komponentu analizē ordinācijas asis izskaidroja 41% no sūnu sugu sadales. Lielāka sūnu sugu bagātība saistīta ar platlapju koku klātbūtni, it īpaši ar osi, liepu un ozolu. Arī vispārējās lineārās analīzes rezultāti rādīja, ka gan kopējais epifītu skaits, gan indikatorsugu skaits bija lielāks ošu audzēs. Pētījumā konstatētas visas mežiem raksturīgās sūnu sugu dzīves stratēģijas un dzīves formas. Visvairāk pārstāvētās sūnu dzīves formas bija gluds klājiens, augsta velēna un raupjš klājiens. Savukārt no sūnu dzīves stratēģijām dominēja daudzgadīgi palicēji, daudzgadīgi konkurenti, kā arī daudzgadīgas ceļotājsugas.