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A contribution to the bryoflora of Moricsala Island Nature Reserve, Latvia

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Abstract: Changes in the bryophyte flora in the Moricsala Island Nature Reserve over a 80-year period were determined using historical records and recent data. Detailed studies of the bryoflora on Moricsala were published in 1931 and 1979. A recent study was carried out starting in 2006, in which bryophytes were recorded separately on different substrates. In total, 182 taxa have been found in the study area, including 25 rare and WKH indicator species. The highest species richness occurs on the forest floor. Since 1931, much of the previous meadow habitat has overgrown to forest. Forests have become more shaded and substrate diversity has likely increased, leading to an increased number of epiphytic and epixylic species. Nine meadow species have become extinct in the study area.

Kokkuvõte: Moricsala saare looduskaitseala (Läti) brüofloorast

Artikkel käsitleb 80 aasta jooksul toimunud muutusi Moricsala saare brüoflooras. Saare brüofloorat uuriti aastatel 1931, 1979 ja 2006. Kokku on leitud 82,3 ha suuruselt saarelt 182 samblataksonit, nende seas 25 haruldast ja metsade väärislupaikade tunnusliiki. Suurim liigirikkus valitseb maapinna sammalde hulgas. Kaheksakümne aasta jooksul on suur osa endistest niitudest metsastunud. Üheksa niiduliiki on saarelt kadunud. Metsad on muutunud varjulisemateks ja epifüütsete ning epiksüülsete sammalde arvu kasv viitab substraatide mitmekesisuse suurenemisele.

INTRODUCTION

Bryophytes are commonly used as indicators of old growth forest continuity (Fritz et al., 2008), as they are dependent on specific substrates present only in these habitats, such as coarse woody debris in different stages of decay (Ódor et al., 2006; Frego, 2007). Old forests support a high diversity of different habitat types and microniches, and thus they maintain a greater number of bryophyte species (Fenton & Bergeron, 2008). Composition of bryophyte communities in mature forest can change over time due to disturbances (Jonsson & Esseen, 1990). Long-term successions of vascular plant communities have been studied previously (Nygaard & Ødegaard, 1999; Widenfalk & Weslien, 2008), but natural successions of bryophyte communities are still poorly known (Uotila & Kouki, 2005). The reasons for this are the lack of detailed studies that have been made in the past and inability to repeat surveys in the same area (coordinates of plots not known and habitat degraded).

The Moricsala Island Nature Reserve, established in 1912, is the oldest protected nature area in Latvia. At the time of initiation of protection, a large part of the island was used as meadow and pasture (Kupffer, 1931), but much of this area has now reforested naturally (Laiviņa & Laiviņš, 1980). The first detailed research on the bryophyte flora of Moricsala Island was conducted by the botanist K. R. Kupffer in 1909–1931 (Kupffer, 1931). During the period of 1974–1979, the flora was again surveyed (Āboliņa et al., 1979; Laiviņa & Laiviņš, 1980). Thus, the area offers an excellent opportunity to study succession in various forest habitats. We conducted our research on Moricsala Island in 2006–2010 (preliminary results have been published in Madžule & Brūmelis, 2008; Mežaka et al., 2009). The goal of the present study was to describe changes in the bryophyte flora on Moricsala Island during the last 100 years.

MATERIAL AND METHODS

Study area

The Moricsala Nature Reserve is located in western Latvia (E 22°7´47´´; N 57°11´35´´). It includes two islands (Moricsala (82.31 ha) and

Lielalksnīte Island (31.11 ha), and part of Usmas Lake, called Luziķērte (704.71 ha). The elevation is 40–60 m above sea level. The mean annual temperature is 5.5–5.8 °C and the precipitation is 700–800 mm per year (Zelčs, 1998).

The forests of Moricsala Island mainly consist of boreal forests, mixed broad-leaved forests, which are dominated by *Tilia cordata* and *Quercus robur*, *Alnus glutinosa* swamp forests, and oak forests. The Moricsala Nature Reserve includes also *Betula pendula* and *Alnus glutinosa* stands, which are located along the island shores. The greater part of forest stands are dominated by *Quercus robur* (45 ha), *Alnus glutinosa* (24.8 ha), *Betula spp.* (9.5 ha), *Tilia cordata* (2.2 ha), and *Populus tremula* (0.4 ha). The coniferous forest stands are dominated by *Pinus sylvestris* (12.0 ha) and *Picea abies* (4.0 ha) (Reihmanis, 2009).

Methods

Data were obtained from three periods (1909–1931, 1973–1979, and 2006–2010). Data from the first two periods were published in Kupffer (1931), Āboliņa et al. (1979), and Laiviņa & Laiviņš (1980). In the first study, lists of species were given separately for 26 vegetation types that were relatively homogenous in forest structure. A map of these types was provided (Fig. 1). In the second, a geographical grid (25×25 m) was used to group records. Vegetation was classified into 13 types according to dominant tree species and vegetation form. Maps from the two studies were overlain, to determine changes in vegetation types over time. In the recent work, plots were established with replication in each of the vegetation types of Kupffer (1931). All forest types except willow thicket and sedge meadows occurring on Moricsala Island were studied in the recent paper. Seventeen sampling plots were established in previous meadows (Fig. 1). In the present study bryophytes were collected from 290 forest floor layer microplots (size 1×1 m), 400 logs and 293 living tree stems in 63 sampling plots (size 25×25 m) (Fig. 1). Five microplots were established on anthropogenic substrates, such as roofs of sheds and footpaths. These were considered as epigeic microplots. In earlier studies, records were not grouped separately by substrate. We divided the species listed by Kuppfer (1931) and Āboliņa et al. (1979) into two groups – (1) epigeic and (2) epixylic & epiphytic. Nomenclature for mosses follows Hill et al. (2006) and for liverworts, Grolle & Long (2000).

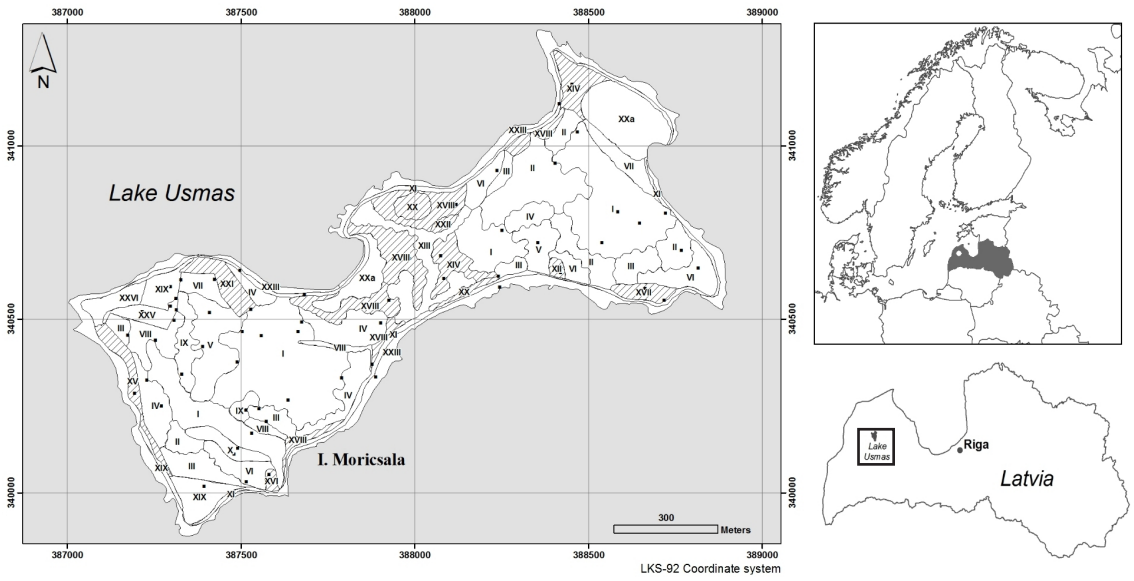

Fig. 1. Location of Moricsala Island and sampling plots (•). Previous meadows that are overgrown with forest are striped. Map of vegetation types made by Kupffer (1931), explanation of polygon numbers given in Table 1.

RESULTS

Kupffer recognized 26 vegetation types in 1931, while later, only 13 vegetation types were recognized by Laiviņa & Laiviņš (1980) (Table 1). Four vegetation types used by Kupffer were each separated into two. For example, Dry oak forest with rich herb layer and Dry broadleaved forest with medium rich herb layer were each differentiated into Oak forest and Oak-lime forest by Laiviņa & Laiviņš (1980). Boggy mixed deciduous forest was split into two groups based on the dominant tree species – Spruce-black alder forest and Birch-spruce forest. Moist fen was differentiated into Willow thicket and Sedge meadow. However, most of Kupffer's vegetation types were joined together into types by Laiviņa & Laiviņš (1980). For example, Moist swampy deciduous forest and Wet swamp forest were both grouped as Broadleaved-black alder forest. Most meadow types have now become forest, for example, Dry shrubby hay meadow changed to Oak-lime forest, and Moist hay meadow to Oak-pine forest.

A total of 182 taxa have been recorded on Moricsala Island, including 150 mosses and 32 liverworts (Table 2), which amounts to 30% of all bryophyte species in Latvia (Āboliņa, 2001). An incomplete list was previously published (Mežaka et al., 2009) in a local journal that is not freely available, and therefore a list is included here. Seventy seven species were found in all three of the studied periods, 54 species were recorded only in earlier studies, and 29 species represented new records. Twenty two species were found in the both recent study and in one of the previous studies (Kupffer, 1931; Āboliņa et al., 1979).

Table 1. Classification of vegetation types on Moricsala Island in previous studies by Kupffer (1931) and Laiviņa & Laiviņš (1980)

Kupffer, 1909–1930	Laiviņa & Laiviņš, 1980
I Dry oak forest with rich herb layer	Oak forest & Oak-lime forest
II Dry broadleaved forest with medium rich herb layer	Oak forest & Oak-lime forest
III Dry deciduous forest with medium rich herb layer	Oak-lime forest
XV Dry bushy hay meadow	Oak-lime forest
VI Dry mixed pine-broadleaved forest	Oak-pine forest
XIII Young mixed deciduous-pine forest (in previous meadow)	Oak-pine forest
XIV Dry shrubby meadow	Oak-pine forest
XVI Dry grass and herb meadow	Oak-pine forest
IV Dry mixed broadleaved-coniferous forest	Broadleaved-spruce forest
V Dry mixed spruce-broadleaved forest	Broadleaved-spruce forest
XII Mixed forest pioneer stage (in previous forest fire)	Aspen forest
VII Moist swampy deciduous forest	Broadleaved-black alder forest
VIII Wet swamp forest	Broadleaved-black alder forest
IX Moist mixed spruce-deciduous forest	Spruce-black alder forest
X Boggy mixed deciduous forest	Spruce-black alder forest & Birch-spruce forest
V Dry mixed spruce-broadleaved forest	Birch-spruce forest
XVII Moist hay meadow	Birch forest
XVIII Moist grass meadow	Birch forest
XXII Boggy heath	Birch forest
XI Island coast forest	Black alder forest
XXIII Shore vegetation	Black alder forest
XXIV Littoral zone	Black alder forest
XX Moist fen	Willow thicket & Sedge meadow
XIX Moist grass hay meadow	Sedge meadow
XXI Wet hay meadow	Sedge meadow
XXV Pasture on ploughed forest soil	Cultural landscape
XXVI Cultural landscape (including garden, tilth, courtyard, dump, road, ditches, fence, and roof)	Cultural landscape

Table 2. Bryophyte species recorded on Moricsala Island in the three studied periods. Bold – rare, protected and WKH indicator species (Āboliņa, 1994; Regulations of the Cabinet of Ministers, 2000; Ek et al., 2002). Substrates: G – epigeic, X – epixylic, P – epiphytic, T – epixylic & epiphytic. Study period: a – 1909–1930, Kupffer (1931); b – 1973–1979, Āboliņa et al. (1979); c – 2006–2010, authors, Mežaka et al. (2009).

	Study period		
Species name	a	b	c
BRYOPHYTA			
Amblystegium serpens (Hedw.) Schimp.	T	G,T	G,X,P
Amblystegium subtile (Hedw.) Schimp.	T	G	
***Anomodon attenuatus* (Hedw.) Huebener**			P
***Anomodon longifolius* (Schleich. ex Brid.) Hartm.**	T		G,P
***Anomodon viticulosus* (Hedw.) Hook. & Taylor**	T		P
***Antitrichia curtipendula* (Hedw.) Brid.**	T	T	X,P
Atrichum undulatum (Hedw.) P. Beauv.	G	G	G,P
Aulacomnium androgynm (Hedw.) Schwägr.	G,T	G,T	G,X,P
Aulacomnium palustre (Hedw.) Schwägr.	G	G	G
Barbula convoluta Hedw.			G
Barbula unguiculata Hedw.		G	G
Brachytheciastrum velutinum (Hedw.) Ignatov & Huttunen	G	G,T	G,X,P
Brachythecium albicans (Hedw.) Schimp.		G	G,X
Brachythecium campestre (Müll. Hal.) Schimp.			G,P
***Brachythecium mildeanum* (Schimp.) Schimp.**		G	
Brachythecium rutabulum (Hedw.) Schimp.	G,T	G,T	G,X,P
Brachythecium salebrosum (Hoffm. ex F. Weber & D. Mohr) Schimp., nom. cons.	G	G,T	G,X,P
Bryoerythrophyllum recurvirostrum (Hedw.) P.C. Chen	G	G	
Bryum argenteum Hedw.		G	G
Bryum caespiticium Hedw.	G	G	G
Bryum capillare Hedw.	G	G	G
Bryum moravicum Podp.			G,X,P
***Bryum neodamense* Itzigs.**	G	G	
Bryum pseudotriquetrum (Hedw.) P.Gaertn. et al.			G,X
Bryum pseudotriquetrum var. bimum (Schreb.) Lilj.	G	G	
Bryum rubens Mitt.			G
Callicladium haldanianum (Grev.) H.A. Crum	G	T	
Calliergon cordifolium (Hedw.) Kindb.	G	G,T	G,X,P
Calliergon giganteum (Schimp.) Kindb.	G	G	
Calliergonella cuspidata (Hedw.) Loeske	G	G,T	G,X,P
Calliergonella lindbergii (Mitt.) Hedenäs	G	G	
Campylium stellatum (Hedw.) Lange & C.E.O. Jensen	G	G	G
Campylophyllum sommerfeltii (Myrin) Hedenäs		G	

Table 2 (continued)

Species name	Study period a	b	c
Ceratodon purpureus (Hedw.) Brid.	G	G	G
Cirriphyllum piliferum (Hedw.) Grout		G,T	G,X
Climacium dendroides (Hedw.) F. Weber & D. Mohr	G	G,T	G,X,P
Cratoneuron filicinum (Hedw.) Spruce	G	G	
Dicranella cerviculata (Hedw.) Schimp.	G	G	X
Dicranella heteromalla (Hedw.) Schimp.	G	G	G
Dicranella varia (Hedw.) Schimp.	G	G	
Dicranum bonjeanii De Not.	G	G	
Dicranum flagellare Hedw.	T	T	G,X
Dicranum fuscescens Sm.			G
Dicranum majus Sm.	G	G,T	G,X
Dicranum montanum (Hedw.)	T	T	G,X,P
Dicranum polysetum Sw. Ex anon	G	G	G,X
Dicranum scoparium Hedw.	G	T	G,X,P
***Dicranum viride* (Sull. & Lesq.) Lindb.**			P
Distichium capillaceum (Hedw.) Bruch & Schimp.			G
Ditrichum flexicaule (Schwägr.) Hampe			G,X
Drepanocladus aduncus (Hedw.) Warnst.	G	G,T	
Drepanocladus polygamus (Schimp.) Hedenäs		G	
***Drepanocladus sendtneri* (Schimp. Ex H.Müll.) Warnst.**		G	
Encalypta streptocarpa Hedw.		G	
Eurhynchiastrum pulchellum (Hedw.) Ignatov & Huttunen		G	
Eurhynchium angustirete (Broth.) T.J. Kop.		G,T	G,X,P
Eurhynchium striatum (Hedw.) Schimp.	G,T	G,T	G,X,P
Fissidens adianthoides Hedw.		G	X
Fissidens taxifolius Hedw.			G,P
Funaria hygrometrica Hedw.	G	G	G
Grimmia pulvinata (Hedw.) Sm.		G	G
***Helodium blandowii* (F. Weber & D. Mohr) Warnst.**	G	G	
Herzogiella seligeri (Brid.) Z. Iwats.	T	T	G,X,P
***Homalia trichomanoides* (Hedw.) Brid.**	T	T	G,X,P
Homalothecium lutescens (Hedw.) H.Rob.			G,X,P
Homalothecium sericeum (Hedw.) Schimp.	T	T	G,X,P
Homomallium incurvatum (Schrad. ex Brid.) Loeske		T	
Hygroamblystegium varium (Hedw.) Mönk.		G	G,X,P
Hylocomium splendens (Hedw.) Schimp.	G	G,T	G,X,P
Hypnum cupressiforme Hedw.	G,T	T	G,X,P

Table 2 (continued)

Species name	Study period a	b	c
***Hypnum imponens* Hedw.**	T	G	
Hypnum pallescens (Hedw.) P. Beauv.		T	X
***Isothecium alopecuroides* (Lam. ex Dubois) Isov.**	T		G,P
Leptobryum pyriforme (Hedw.) Wilson	G	G	
Leptodictyum riparium (Hedw.) Warnst.	G,T	G,T	P
Leskea polycarpa Hedw.			X,P
Leucodon sciuroides (Hedw.) Schwägr.	T	T	G,X,P
Mnium hornum Hedw.		G,T	G,X,P
Mnium stellare Hedw.			G,P
***Neckera complanata* (Hedw.) Huebener**	T	T	X,P
***Neckera pennata* Hedw.**	T	T	P
Orthotrichum affine Schrad. ex Brid.	T	G	X
Orthotrichum gymnostomum Bruch ex Brid.	T	G	
Orthotrichum patens Bruch & Brid.	T		
Orthotrichum speciosum Nees	T	G,T	X,P
Oxyrrhynchium hians (Hedw.) Loeske		G	G,X,P
Oxyrrhynchium speciosum (Brid.) Warnst.			G,P
Plagiomnium affine (Blandow ex Funck) T.J. Kop.	G	G,T	G,X,P
Plagiomnium cuspidatum (Hedw.) T.J. Kop.	G	G,T	G,X,P
Plagiomnium elatum (Bruch & Schimp.) T.J. Kop.	G	G	
Plagiomnium ellipticum (Brid.) T.J. Kop.		G,T	G,X,P
Plagiomnium medium (Bruch & Schimp.) T.J. Kop.	G	T	
Plagiomnium undulatum (Hedw.) T.J. Kop.	G	T	G,X
Plagiothecium cavifolium (Brid.) Z. Iwats.	T	G	G,X,P
Plagiothecium denticulatum (Hedw.) Schimp.	G,T	G	G,X,P
Plagiothecium laetum Schimp.	T	G,T	G,X,P
***Plagiothecium latebricola* Schimp.**	T	T	G,X,P
Plagiothecium nemorale (Mitt.) A. Jaeger		T	
Plagiothecium succulentum (Wilson) Lindb.	T	G,T	
Platygyrium repens (Brid.) Schimp.	T	G	G,X,P
Pleurozium schreberi (Willd. ex Brid.) Mitt.	G	G,T	G,X,P
Pohlia cruda (Hedw.) Lindb.		G	G
Pohlia nutans (Hedw.) Lindb.	G	G,T	G,X
Pohlia wahlenbergii (F. Weber & D. Mohr) A.L. Andrews	G	G	
Polytrichastrum formosum (Hedw.) G.L. Sm.	G	G	
Polytrichastrum longisetum (Sw. ex Brid.) G.L. Sm.	G	G	
Polytrichum commune Hedw.	G	G	G,X

Table 2 (continued)

Species name	Study period a	b	c
Polytrichum juniperinum Hedw.	G	G	X
Pseudobryum cinclidioides (Huebener) T.J. Kop.		G	G,X,P
***Pseudocalliergon lycopodioides* (Brid.) Hedenäs**	G	G	
Pseudoscleropodium purum (Hedw.) M. Fleisch.	G	G	
Ptilium crista-castrensis (Hedw.) De Not.	G	G	X
Pylaisia polyantha (Hedw.) Schimp.	T	T	X,P
Rhizomnium punctatum (Hedw.) T.J. Kop.	G	G,T	G,X,P
Rhodobryum roseum (Hedw.) Limpr.	G	G	G,X,P
Rhytidiadelphus squarrosus (Hedw.) Warnst.	G	G	G
Rhytidiadelphus subpinnatus (Lindb.) T.J. Kop.		G	
Rhytidiadelphus triquetrus (Hedw.) Warnst.	G	G	G,X,P
Sanionia uncinata (Hedw.) Loeske	G,T	G	G,X,P
Schistidium apocarpum (Hedw.) Bruch & Schimp.		G	G
Sciuro-hypnum oedipodium (Mitt.) Ignatov & Huttunen	G,T	G,T	G,X,P
Sciuro-hypnum plumosum (Hedw.) Ignatov & Huttunen, nom. cons.	T		
Sciuro-hypnum populeum (Hedw.) Ignatov & Huttunen			P
Sciuro-hypnum reflexum (Starke) Ignatov & Huttunen	T	T	
Scorpidium cossonii (Schimp.) Hedenäs	G	G	
Sphagnum angustifolium (C.E.O. Jensen ex Russow) C.E.O. Jensen	G	G	
Sphagnum capillifolium (Ehrh.) Hedw.	G	G	X
Sphagnum centrale C.E.O. Jensen	G	G	
Sphagnum fallax (H. Klinggr.) H. Klinggr.		G	G
Sphagnum fimbriatum Wilson		G	
Sphagnum girgensohnii Russow		G	G,X
Sphagnum magellanicum Brid.		G	
Sphagnum palustre L.	G	G	G,X
Sphagnum riparium Ångström	G	G	
Sphagnum russowii Warnst.	G	G	G,X
Sphagnum squarrosum Crome	G	G	G,X
Sphagnum subsecundum Nees	G	G	
Sphagnum teres (Schimp.) Ångström		G	
Straminergon stramineum (Dicks. ex Brid.) Hedenäs		G	
Syntrichia ruralis (Hedw.) F. Weber & D. Mohr	G	G	
Tetraphis pellucida Hedw.	G,T	G,T	G,X,P
Thuidium assimile (Mitt.) A. Jaeger	G		
Thuidium delicatulum (Hedw.) Schimp.	G	G,T	G,X
Thuidium recognitum (Hedw.) Lindb.	G	G	

Table 2 (continued)

Species name	Study period a	b	c
Thuidium tamariscinum (Hedw.) Schimp.	G	G	G,X
Tortula subulata Hedw.	G	G	
Tortula truncata (Hedw.) Mitt.			G
***Ulota crispa* (Hedw.) Brid.**	T	T	G,X,P
Warnstorfia exannulata (Schimp.) Loeske		G	
***Zygodon rupestris* Schimp. ex Lorentz**			P
MARCHANTIOPHYTA			
***Barbilophozia attenuata* (Mart.) Loeske**			X
Blepharostoma trichophyllum (L.) Dumort.	G	T	X
Calypogeia azurea Stotler & Crotz	G	G	G,X
Calypogeia neesiana (C. Massal. & Carestia) K. Müller.Frib.	G	G,T	G,X
Cephalozia bicuspidata (L.) Dumort.		T	G,X,P
Chiloscyphus pallescens (Ehrh. ex Hoffm.) Dumort.			G,X,P
Chiloscyphus polyanthos (L.) Corda		T	
Cladopodiella fluitans (Nees) Jörg.			G
Frullania dilatata (L.) Dumort.	T	T	X,P
***Jamesoniella autumnalis* (DC.) Steph.**		T	G,X,P
Jungermannia atrovirens Dumort.	G,T	T	
***Jungermannia leiantha* Grolle**			X
***Jungermannia sphaerocarpa* Hook.**			X
Lepidozia reptans (L.) Dumort.	G,T	T	G,X,P
Lophocolea bidentata (L.) Dumort.			G,X,P
Lophocolea heterophylla (Schrad.) Dumort.	G,T	T	G,X,P
Lophocolea minor Nees		G	
Lophozia sp.			X
Marchantia polymorpha (L.)	G,T	G	G
***Metzgeria furcata* (L.) Dumort.**	T	T	X,P
Nowellia curvifolia (Dicks.) Mitt.	T	T	G,X
Pellia endiviifolia (Dicks.) Dumort.			G,X,P
Pellia neesiana (Gottsche) Limpr.			G
Pellia sp.	G	G	
Plagiochila asplenioides (L. emend. Taylor) Dumort.	G	G,T	G,X,P
Plagiochila porelloides (Torrey ex Nees) Lindenb.			P
***Preissia quadrata* (Scop.) Nees**	G	G	
Ptilidium pulcherrimum (Weber) Vain.	T	T	X,P
Radula complanata (L.) Dumort.	T	T	G,X,P
Riccardia latifrons (Lindb.) Lindb.	T	T	X
***Riccardia palmata* (Hedw.) Carruth.**	T	G	X
Riccia sp.			X

The species list includes 25 protected and WKH indicator bryophyte species. A similar number of signal species was recorded in each study period (17 species by Kupffer (1931), 16 species by Āboliņa et al. (1979), 19 species in the recent study), but the species composition differed among them. Nine signal species were recorded in all investigations; four species were found exclusively in both earlier studies (1909–1931, 1973–1979), and five species were recorded only in the present work (during 2006–2010). Seven WKH indicator species (*Antitrichia curtipendula*, *Homalia trichomanoides*, *Metzgeria furcata*, *Neckera complanata*, *N. pennata*, *Plagiothecium latebricola, Ulota crispa*) were found in all three periods. Three WKH indicator species (*Anomodon attenuatus*, *Barbilophozia attenuata*, *Jungermannia leiantha*), and three rare and protected species in Latvia (*Dicranum viride*, *Zygodon rupestris*, *Jungermannia sphaerocarpa*) were found only in the recent study.

In all three studies, the highest species richness was recorded on the forest floor layer (Fig. 2): Kupffer (1931) – 83 species, Āboliņa et al. (1979) – 112 species, in the recent study – 97 species. Bryophyte richness on woody substrates was the lowest in the Kupffer (1931) study (48 species). Āboliņa et al. (1979) found 65 species on woody substrates compared to 106 species (92 species on logs and 71 species on living tree stems) in the recent study.

To show the dynamics of the bryophyte flora in each vegetation type (vegetation types of Laiviņa & Laiviņš, 1980) during last 100 years, the numbers of species found only in one of the study periods were determined (Fig. 3). It was assumed that species found only by Kupffer (1931) had been lost and that species found only in the recent study were new to the particular vegetation type. During the last 100 years, significant changes in the bryophyte flora occurred in all 13 vegetation types. The largest numbers of new species were recorded in Birch forest, Oak-lime forest and Broadleaved-spruce forest vegetation types (accordingly 47, 43, and 33 new records). The Birch forest type had developed on meadows, but Broadleaved-spruce forest and largest part of Oak-lime forest were also described as forests by Kupffer (1931) (Table 1). The new species in all three vegetation types were mainly liverworts such as *Calypogeia azurea*, *Cephalozia bicuspidata*, *Chiloscyphus pallescens*, *Jungermannia leiantha*, *Lophocolea bidentata*, and *Riccardia latifrons*.

The largest number of species lost was found in Broadleaved-black alder forest, Sedge meadow and Black alder forest vegetation types (accordingly 18, 17, and 13 lost species). The Black alder forest type had largely developed in non-wooded coastal areas (Table 1). Of these lost species, many (e.g. *Bryum caespiticium*, *Bryum pseudotriquetrum* var. *bimum*, *Campylium stel-*

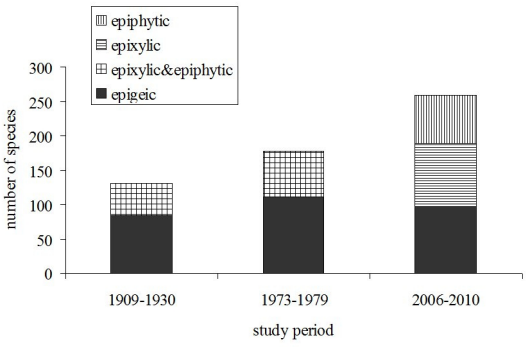

Fig. 2. Total number of bryophyte species found on different substrates in the study periods. Study period: 1909–1930 – Kupffer (1931); 1973–1979 – Āboliņa et al. (1979); 2006–2010 – authors.

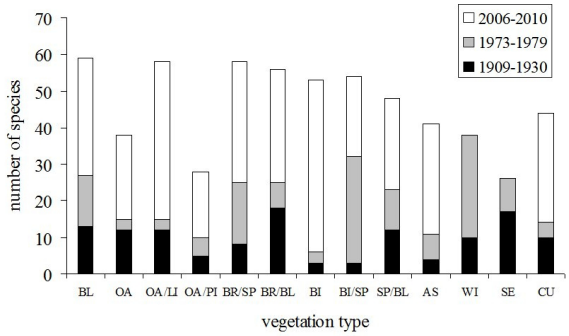

Fig. 3. Number of species found only in one of the study periods in different vegetation types. Vegetation type: BL – Black alder forest; OA – Oak forest; OA-LI – Oak-lime forest; OA-PI – Oak-pine forest; BR-SP – Broadleaved-spruce forest; BR-BL – Broadleaved-black alder forest; BI – Birch forest; BI-SP – Birch-spruce forest; SP-BL – Spruce-black alder forest; AS – Aspen forest; WI – Willow thicket; SE – Sedge meadow; CU – Cultural landscape.

latum, *Plagiomnium elatum*, *Polytrichum juniperinum*, and *Scorpidium cossonii*) were previously found in wet open areas. However, most of the species lost from a particular vegetation type did survive in other types. Nine bryophyte species (*Bryum neodamense*, *Calliergon giganteum*, *Cratoneuron filicinum*, *Helodium blandowii*, *Pohlia wahlenbergii*, *Preissia quadrata*, *Pseudocalliergon lycopodioides*, *Scorpidium cossonii*, *Sphagnum centrale*) that are no longer found on the island, previously occurred only in wet meadows with rich herb and grass layer or in fens during the period of 1909–1931 (Kuppfer, 1931). The presence of these species was assessed as uncertain during the period of 1973–1979, and only in habitats without tree layer (Āboliņa et al., 1979).

DISCUSSION

Since founding of the reserve on Moricsala Island, a denser understory of spruce, lime and maple has developed (Kupffer, 1931; Brūmelis et al., 2011). Thus, the open forests have become more shaded. Also, the larger part of all previous meadows has overgrown to forest. A new vegetation type (Aspen forest) has established in burnt birch stand (Laiviņa & Laiviņš, 1980). However, three grassland types and cultural lands have not changed to forest. In moist meadows, shore vegetation and in the littoral zone, periodic tree death is caused by fluctuations of water level in Usma Lake (Reihmanis, 2009). The observed changes in the bryophyte flora can be explained by natural succession. Overgrowth of wet meadows has led to the loss of nine species, such as *Helodium blandowii*, *Pseudocalliergon lycopodioides*, and *Scorpidium cossonii,* as all of the vegetation plots where these species were previously found have now overgrown to forest.

Changes in species composition occurred not only in overgrown meadows (like Birch forest), but in vegetation types that have been forest during the last 100 years also, for example, in Oak-lime forest and in Broadleaved-spruce forest. Of the twenty nine species representing new records, many, for example, *Barbilophozia attenuata*, *Dicranum viride*, *Jungermannia leiantha*, and *Zygodon baumgartneri* are epiphytic or epixylic bryophytes. In forests, substrate diversity has likely increased. Tree death caused by natural disturbances such as severe storms in 1967 and 1969 (Laiviņa & Laiviņš, 1980) and fluctuations in water level in Usma Lake during 1978–1981 (Reihmanis, 2009) were observed to provide large amounts of coarse woody debris. Before the initiation of protection of Moricsala Island mortality due to factors such as disease and thinning can be considered to have continuously increased dead wood amounts. However, there is a strong possibility that dead wood was then removed for firewood. This can explain the increased epixylic bryophyte species richness in the later studies. Natural successions in forests lead to higher tree density and diameter, more diverse layer structure, and mixed forest stands (Fenton & Bergeron, 2008), leading to a greater number of microniches for epiphytic species.

Among the epigeic bryoflora found only recently, only two species, *Bryum rubens* and *Riccia* sp., were restricted to sampling plots on previously managed lands. Other new epigeic species, like *Bryum moravicum*, *Ditrichum flexicaule*, and *Cladopodiella fluitans*, were found in several habitats.

Some species, of course, may have been missed in the earlier studies. *Anomodon attenuatus*, an epiphytic species, was recorded only in the recent study. This is a comparatively large moss and it is unlikely that this species would have been missed in the surveys conducted by the botanists. This might not be the case for other newly recorded epiphytes, like *Dicranum viride* and *Zygodon rupestris*, which are very small and might simply not have been found. In general, most of the new species (*Brachythecium campestre*, *Leskea polycarpa*, *Oxyrrhynchium speciosum*, *Chiloscyphus pallescens*) require shaded conditions and their absence in the earlier study might be explained by a more open canopy available. In forests, sun loving species (for example, *Bryum moravicum*, *Bryum rubens*, *Fissidens taxifolius*) occur only sporadically on more exposed tree stems, on fallen tree roots, and in newly formed pits and mounds after small-scale disturbances due to canopy gap formation (von Oheimb et al., 2007). Mostly, the new records were found in more than one forest type, and the increased richness of the flora in the recent study can be explained by a wider diversity of the substrates (for example, dead wood and large diameter trees) that developed after abandonment of grazing.

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