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Effect of grazing on plant diversity of coastal meadows in Estonia

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Vascular plant and bryophyte species richness, and bryophyte diaspore bank were studied in 14 Estonian coastal meadows that had been under two different grazing pressures for ca. 10 years. The aim of the study was to compare the effects of grazing intensity on the diversity of these plant groups, and on the bryophyte diaspore bank. The results showed that (1) intensive grazing increased bryophyte diversity, but not that of vascular plants or the diaspore bank; (2) vascular plant diversity was suppressed by litter cover; (3) vascular plant and bryophyte diversities were positively correlated; and (4) the species composition remained unaffected by grazing intensity.

Introduction

Coastal meadows surrounding the Baltic Sea started to form thousands of years ago, after the continental ice sheet had withdrawn and the land began to rise from the sea. During the post-glacial land uplift, coastal meadows have been continually migrating towards the sea. The isostatic land uplift in the Baltic Sea region is currently ca. 1–9 mm per year (Ekman & Mäkinen 1996).

According to the duration and frequency of flooding, coastal meadows can be divided into saline and suprasaline zones (Laasimer 1965, Rannap *et al*. 2004). These zones are, on average, less than 50 m wide, but may reach a width of hundreds of meters, the altitude being usually < 1 m a.s.l. (Rannap *et al*. 2004, Ratas & Rivis 2007). Without grazing by animals, primary meadows would soon be taken over by reed (*Phragmites australis*) and woody plants, mainly *Salix* spp. and *Juniperus communis*. Cattle husbandry in the region of modern Estonia started more than 5000 years ago, presumably in coastal areas (Kriiska 2004). Consequently, the coastal meadows in Estonia are mainly semi-natural communities that require continuous management.

The last 50 years witnessed widespread degradation of coastal meadows due to land use changes and the cessation of traditional management, such as grazing and mowing. During the second half of the 20th century, the area of managed coastal meadows in Estonia decreased from 29 000 ha to 8000 ha (Luhamaa *et al*. 2001). Abandonment of formerly grazed coastal wetland grasslands in Estonia also reduced the area of grasslands of special conservation value (Burnside *et al*. 2007). Large losses have also occurred in Sweden and Finland (Jutila 2001, Ottvall & Smith 2006). This habitat type has become endangered throughout Europe (EU Habitat Directive 92/43/EEC) and more research is needed to ensure its protection. Restoration of coastal meadows started in Estonia at the end of the 20th century. Supporting cattle husbandry and mowing has led to an improvement of many coastal meadows (Kose *et al*. 2011).

Coastal meadows are characterized by a high plant diversity: 390 vascular plant species (Pärtel *et al*. 2007), and 100 bryophyte species (authors' unpubl. data), comprising 26% of the Estonian vascular plant flora and 17% of the Estonian bryoflora, have been found in the Estonian coastal meadows. Coastal meadows are the primary habitat for several rare or endangered plant and animal species (Roosaluste 2004, Rannap *et al*. 2007, Rautiainen *et al*. 2007), and serve as feeding or breeding sites for many birds (Ottvall & Smith 2006), which are threatened by their decline. In addition to several protected vascular plant species, one protected bryophyte species, *Bryum marratii*, grows in the Estonian coastal meadows. Maintaining the richness of vascular plant and bryophyte species in coastal meadows requires knowledge of the ecological demands of these species, and possible effects of meadow management.

Although numerous studies on the influence of mowing and grazing on vascular plant richness in different types of meadows were carried our, very few concerned bryophytes (Takala *et al*. 2012), and while the effects of grazing on coastal meadow vascular plant vegetation gained some attention (Jutila 1997, 1998, 1999, 2001, Grace & Jutila 1999, Dupre & Dieckmann 2001, Loucougaray *et al*. 2004), same cannot be said about bryophytes. However, these effects should be studied, because bryophytes are known to suppress germination and juvenile growth of several vascular plant species that rely mainly on seed dispersal (Keizer *et al*. 1985, van Tooren 1988, Zamfir 2000, Otsus & Zobel 2004, Soudzilovskaia *et al*. 2011). On the other hand, bryophytes can promote germination or juvenile growth of some species. Moss cover may facilitate vascular plants by maintaining high soil moisture and provide nutrients upon decomposition (van Tooren *et al*. 1987, Longton 1992). In addition, the bryophyte layer provides a habitat for many invertebrates (Gerson 1982). Therefore, bryophytes play an important role also in coastal meadow communities.

We aimed to fill the above-mentioned gaps in knowledge by comparing the responses of both vascular plants and bryophytes to grazing intensity in coastal meadows.

Our aims were (1) to determine how grazing intensity, litter, and bryophyte cover affect the diversity of vascular plant and bryophyte diversity; and (2) to find out how the diaspore bank of bryophytes in coastal meadows is affected by management intensity.

Material and methods

Study area

Our study sites were located in the Matsalu National Park on the western coast of Estonia, and on the island of Saaremaa, (58°23´–58°44´ and 23°40´–32°74´; Fig. 1). The two regions have a similar soil type (coastal glaysol; Kask 1988) and climate, which is relatively mild owing to the proximity to the sea. The mean temperature is 16.5 °C in July and –4.5 °C in January; the average annual temperature is 5–5.5 °C, and the annual precipitation is 600–650 mm (Jaagus 1999). However, there is a slight difference between the two areas: Occasionally, surface-water salinity of the more closed Matsalu Bay can be low (0.5–6 PSU) and the nutrient levels high due to the inflow of the Kasari River (Kotta *et al*. 2008). The sea around Saaremaa island is more open and the fluctuations in salinity (6–7 PSU) and nutrients are not so great. The study plots were set in the suprasaline zone of the coastal meadows, which are flooded by brackish water only during severe storms.

Data collection and analyses

The data were collected in July 2004 in Matsalu and in August 2005 in Saaremaa. The study contained 14 grazed coastal meadows (seven in Matsalu and seven in Saaremaa; Table 1). Seven of the meadows (3 in Matsalu and 4 in Saaremaa) were grazed more intensively than advised (more than 1 cow per ha) and the remaining seven were grazed weakly (less than 1 cow per ha). The recommended number of cattle on coastal meadows is ca. 1 cow or 2–5 sheep per ha (http://www.keskkonnaamet.ee/public/PLK/Guidlines-

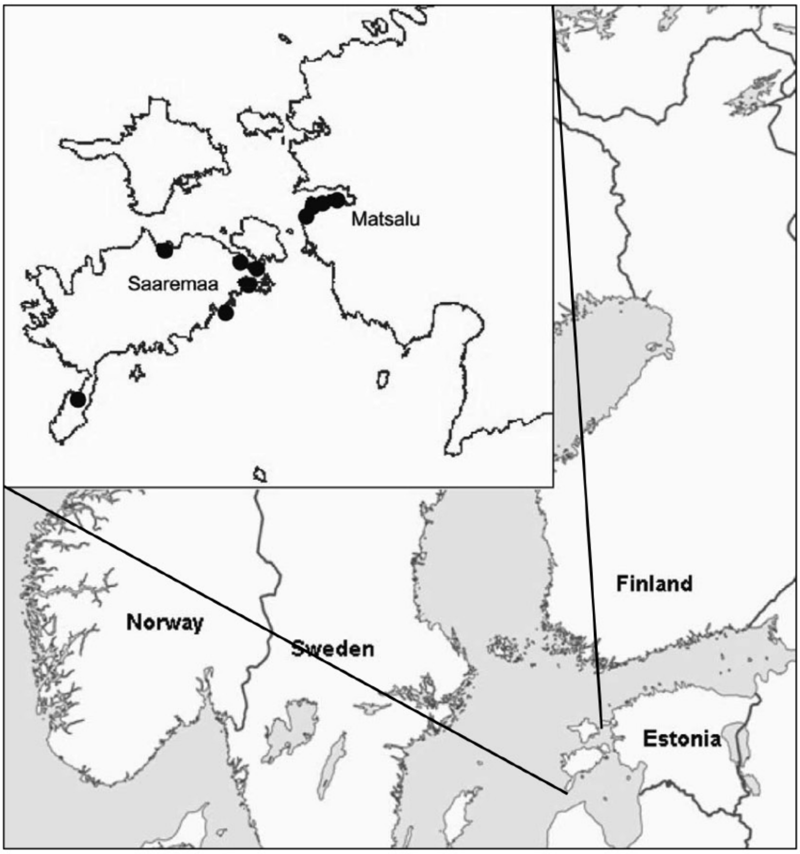

Fig. 1. Locations of study sites. Areas close to each other are merged.

for-Coastal-Meadow-Maintenance.pdf). Data on the management type for the previous 10 years were obtained from the local authorities. The majority of the meadows were grazed regularly up to the end of the 1980s. Since the beginning of the 1990s more than half of the meadows were neglected or with a very low grazing load. The mean area of the studied meadows was 100 ha (range 25–350 ha). A 50 × 50 m homogenous study plot was delimited in each coastal meadow. Ten 1 × 1 m plots were randomly distributed within each larger plot. Bryophyte and vascular plant species, the cover of bryophyte species, and the cover of litter (undecomposed parts of dead plants) were recorded in each 1 m^2 plot and mean values were calculated for each larger plot. The cover of vascular plants was not recorded since it changes much more than bryophyte cover during the vegetation period and due to different grazing pressure. Soil samples from the upper 1 cm layer were taken from five 1 m^2 plots in each meadow to study the bryophyte diaspore bank and measure soil pH. Soil pH varied little among the studied meadows (mean = 7.6, range 6.1–8.3). As the samples were collected only from five 1 m^2 plots in each larger plot, this parameter was excluded from further analysis.

The soil samples were sieved and all visible plant particles removed. About 30 cm^3 of soil from each 1 m^2 plot was spread on Petri dishes with a diameter of 9 cm. The soil was kept moist by spraying with distilled water. The daytime radiation was between 100–110 μmol m^{-2} s^{-1} and the temperature fluctuated between 25–32 °C at daytime and 15–20 °C at night. Germinated bryophytes were classified to species after six months. The number of germinated species was evaluated for each dish, and the mean number of species was calculated for each meadow.

Life history strategy group (during 1992) was specified for each bryophyte species. Spearman's rank-order correlation (ρ) was used to

Table 1. Parameters measured at 14 coastal-meadow sites in Estonia with different grazing intensity. bryo = bryophyte species; vas = vascular plant species; cover in %.

Site	Mean bryo no. per 1 m²	Total bryo no. per site	Mean vas no. per 1 m²	Total vas no. per site	Mean bryo cover per 1 m²	Mean litter cover per 1 m²	Grazing intensity
Matsalu: Keemu 1	5.0	16	14.5	42	9.3	23.6	strong
Matsalu: Mäisaküla 1	6.6	13	17.7	25	7.3	8.4	strong
Matsalu: Näärhi	7.2	22	26.2	41	10.6	3.8	strong
Saarenmaa: Nenu	2.7	6	11.6	28	1.6	9.8	strong
Saarenmaa: Talila	3.0	8	18.9	40	25.1	8.7	strong
Saarenmaa: Ruhve	4.0	7	9.6	20	18	21.5	strong
Saarenmaa: Unguma	5.0	8	14.1	28	14.5	20.3	strong
Mean	**4.8**	**11.4**	**16.1**	**32**	**12.4**	**13.7**	**average strong**
Matsalu: Keemu 2	4.9	21	15.8	36	1.7	25.5	weak
Matsalu: Mäisaküla 2	2.9	8	13.6	32	3.1	32	weak
Matsalu: Saastna	2.9	8	21.1	41	17.8	2.1	weak
Matsalu: Keemu 3	5.5	14	17.5	37	52.1	23.2	weak
Saarenmaa: Rahuste 1	2.3	3	14.7	32	1.8	3.8	weak
Saarenmaa: Rahuste 2	2.0	3	15.8	26	15.1	13.1	weak
Saarenmaa: Parametsa	2.1	4	8.1	17	1.3	25.5	weak
Mean	**3.2**	**8.7**	**15.2**	**31.6**	**13.3**	**17.9**	**average weak**

study the relationships between species richness of vascular plants and bryophytes, and a Mann-Whitney *U*-test was used to compare the species richness, litter, and bryophyte cover of the two regions. General Linear Models (GLM in Statistica 7) were used to study the influence of four predictors on species richness of bryophytes, bryophyte diaspore bank, and vascular plants. Two categorical predictors: 'grazing intensity' (strong and weak grazing) and 'region' (Matsalu and Saaremaa, differing in the surrounding sea-water properties) were used in the model. Also two continuous predictors, 'bryophyte cover' and 'litter cover', were used in the model. The differences in species composition of the plots with different management type were analyzed with Detrended correspondence analysis (DCA).

The taxonomic nomenclature of liverworts follows Schumacker and Váňa (2005), of mosses Hill *et al*. (2006), and of vascular plants Krall *et al*. (2010).

Results

Altogether 50 species of bryophytes were identified in the studied meadows (Table 2). Thirty-five bryophyte species germinated from the diaspore bank, and some of them developed antheridia or archegonia. Eighteen species from the diaspore bank were not recorded in the emergent flora, and 15 species were observed exclusively aboveground. Seventeen species were found in both the diaspore bank and the emergent flora. The emergent flora contained more pleurocarpous species, although acrocarps and pleurocarps were equally represented in the diaspore bank. According to life history strategies (During 1992), perennials dominated aboveground, whereas colonist and shuttle species dominated in the diaspore bank. The most common bryophytes aboveground were *Calliergonella cuspidata*, *Homalothecium lutescens* and *Rhytidiadelphus squarrosus*, and in the diaspore bank *Barbula convoluta*, *Funaria hygrometrica* and *Pohlia nutans*.

A total of 148 vascular plant species was identified in the studied meadows. The most frequent taxa were *Galium verum*, *Festuca rubra, Centaurea jacea*, *Ranunculus acris*, *Galium boreale*, *Achillea millefolium*, *Trifolium pra-*

tense, *Taraxacum* spp., and *Lathyrus pratensis*.

Total species richness per site of above-ground bryophytes was positively correlated with vascular plant richness ($\rho = 0.624$, $n = 14$, $p < 0.02$), but the mean small-scale (1 m^{2}) richness was not.

Only the total species richness of bryophytes was significantly higher in the Matsalu region (*U*-test: $Z = 2.875$, $n = 14$, $p = 0.0036$). The cover of bryophytes and litter did not differ significantly between meadows with different grazing loads (*U*-test, $p > 0.05$).

The GLM analyses showed that the species richness of vascular plants was significantly associated with region and amount of litter cover, and the species richness of bryophytes was significantly associated with region and grazing intensity (Table 3). Higher species richness in both plant groups was in Matsalu. The litter cover had significant negative effect on the richness of vascular plants, but not on the richness of bryophytes. Bryophyte cover showed no association with species richness of the plant groups. Bryophyte richness was significantly positively affected by grazing intensity (Fig. 2).

Species from diaspore bank emerged from 69 plots of the total 70. The mean richness of the diaspore bank for all areas ($n = 14$) was 5.5 (range 1.4–5.8). According to the GLM analyses, there were no significant differences in the mean species richness of the diaspore bank (data not shown).

DCA did not reveal differences in the species composition of the plots with different management types.

Discussion

In most coastal meadows grazing prevents overgrowth by woody plants and reeds and increases plant species richness. Species richness of vas-

Table 2. List of bryophyte species recorded in the emergent flora and in diaspore bank of 14 studied coastal meadow sites in Estonia. The numbers indicate at how many sites the species was found.

Species	Emergent flora	Diaspore bank	Species	Emergent flora	Diaspore bank
Abietinella abietina	0	1	*Dicranella varia*	0	3
Aneura pinguis	3	0	*Didymodon fallax*	0	1
Amblystegium serpens	10	3	*Ditrichum flexicaule*	2	0
Amblystegium subtile	0	1	*Drepanocladus aduncus*	5	1
Atrichum angustatum	0	1	*Drepanocladus polygamus*	3	6
Atrichum tenellum	0	1	*Fissidens adianthoides*	7	3
Barbula convoluta	4	13	*Fissidens osmundoides*	1	5
Brachythecium albicans	4	1	*Funaria hygrometrica*	1	10
Brachythecium mildeanum	2	2	*Homalothecium lutescens*	5	0
Brachythecium rivulare	1	0	*Hygroamblystegium varium*	0	1
Brachythecium rutabulum	5	0	*Hylocomium splendens*	1	0
Brachythecium salebrosum	2	1	*Hypnum lindbergii*	0	4
Bryum argenteum	1	2	*Leptobryum pyriforme*	0	6
Bryum pseudotriquetrum	5	7	*Lophocolea bidentata*	1	0
Bryum sp.	6	10	*Oxyrrhynchium hians*	1	0
Calliergon cordifolium	0	1	*Physcomitrium* sp.	0	1
Calliergonella cuspidata	13	0	*Plagiomnium cuspidatum*	0	1
Campyliadelphus chrysophyllus	2	5	*Plagiomnium ellipticum*	1	0
Campyliadelphus elodes	4	0	*Pohlia nutans*	0	13
Campylophyllum sommerfeltii	3	6	*Pseudocalliergon turgescens*	5	1
Campylium stellatum	7	3	*Pseudoscleropodium purum*	2	0
Ceratodon purpureus	0	1	*Rhytidiadelphus squarrosus*	5	0
Cratoneuron filicinum	0	1	*Scorpidium scorpioides*	3	0
Ctenidium molluscum	4	0	*Thuidium delicatulum*	0	1
Dicranella schreberiana	0	1	*Tortula* sp.	0	7

cular plants in the Estonian coastal meadows is highest in the suprasaline zone (Roosaluste 2004). Our data were collected from two coastal regions: the Matsalu region on the mainland and from the Saaremaa region on an island. Higher species richness of both plant groups was found in the Matsalu coastal meadows. This might be partly explained by the differences in salinity of the adjacent sea water; however, Matsalu National Park is a prominent Ramsar site (*see* http://www.ramsar.org/wetland/estonia) and the number of migrating birds there is much higher than on the Saaremaa island (Leito *et al*. 2003). Since birds can be important dispersal vectors for plants, this might also explain the higher species richness in Matsalu.

Overly intensive grazing or inadequate grazing can cause significant changes in plant cover. Our study revealed different responses of vascular plants and bryophytes to grazing intensity, in a homogenous community type, suprasaline coastal meadow. Our results suggest that species richness of bryophytes is significantly affected by grazing intensity, but grazing intensity has no effect on vascular plant species richness. Jutila (1997) noted that the species richness of vascular plants in seashore grasslands in Finland is greater in areas that are not grazed. By contrast, cessation of grazing for 5–25 years in grasslands in the Finnish interior resulted in a decline in species richness (Luoto *et al*. 2003). In salt marshes in Belgium, grazing by sheep increased plant richness in higher zones but no effect was detected in lower zones (Milotic *et al*. 2010). A study of coastal meadows in the UK demonstrated an increase of vascular plant richness induced by grazing (Ford *et al*. 2012). Dupré and Diekmann (2001) reported greater species richness in grazed coastal meadows than in abandoned meadows in southern Sweden at a small scale (0.01 m^2), but insignificant differences in plots 1 m^2 or larger. It seems that vascular plant richness responds to grazing in different ways depending on the geographical region and meadow type. Vegetation in coastal areas must overcome permanent or occasional flooding by sea (or brackish) water, wave-induced soil erosion, and storm surges. Vegetation in coastal areas can be classified into distinct plant communities according to the intensity of those environmental factors, bedrock type and land relief (Roosaluste 2004). These distinct communities might require different grazing intensity to maintain high species diversity.

Grazing usually favours bryophytes since it reduces vascular plant cover. The effect of management on bryophytes in coastal meadows has not been previously studied, but research in other types of meadows has shown that bryophyte species richness benefits from grazing (During & Willems 1984, Eskelinen & Oksanen 2009). We suggest that a moderate increase in grazing

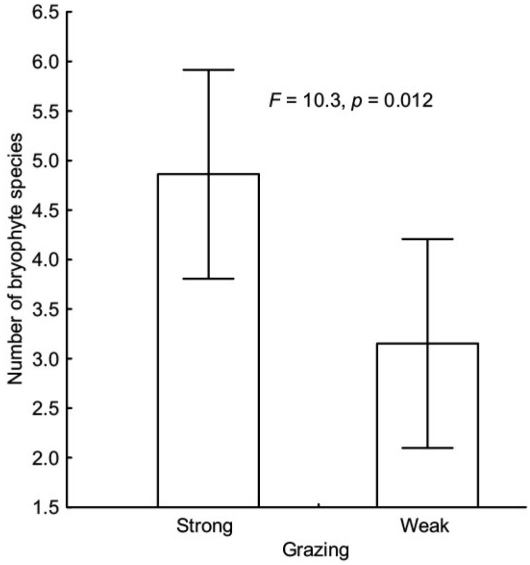

Fig. 2. Effect of grazing intensity on the bryophyte richness according to GLM. Whiskers are 95%CIs.

Table 3. Effects of measured variables on species richness of vascular plants and bryophytes as revealed by the GLM analysis. df = 1, n.s. = not significant.

	F	*p*
Vascular plants (n = 14)		
Bryophyte cover	1.54	n.s.
Litter cover	12.98	0.007
Grazing intensity	0.07	n.s.
Region	11.78	0.009
Region × grazing intensity	0	n.s.
Bryophytes (n = 14)		
Bryophyte cover	1.45	n.s.
Litter cover	0.14	n.s.
Grazing intensity	10.30	0.012
Region	12.64	0.007
Region × grazing intensity	1.03	n.s.

intensity increases the bryophyte diversity on suprasaline coastal meadows.

Our study shows that the vascular plant richness in the Estonian coastal meadows was negatively affected by litter cover, but litter did not affect the bryophyte richness. Peintinger and Bergamini (2006) revealed that litter mass reduced both vascular plant and bryophyte species densities in fen meadows in Switzerland. Standing litter biomass in mountain meadows in Scotland has a negative effect on bryophyte richness, but no effect on vascular plant richness (Virtanen & Crawley 2010). In the old-field communities in USA, litter removal increased the species richness of annual plants, but increased the total vascular plant richness only temporarily (Carson & Peterson 1990). In a study of grasslands in Hungary (Kelemen *et al.* 2012), both living biomass and litter biomass increased vascular plant richness at low amounts but decreased it at high amounts. This indicates that the relation between species richness and the amount of litter depends on the community type and the amount of litter. Higher amount of litter in our study was not caused by lower grazing load. The explanation to this can be that at least some litter was swept off by storms and the decrease of vascular plant richness due to higher litter cover might partly be explained by the effect of brackish water and waves.

The diaspore bank and seed bank analysis can provide insight into potential species diversity and past changes in the habitat. Several studies have revealed that seed banks in grasslands decline with intensified grazing (Bertiller 1992, Marage *et al.* 2006; but *see* Matus *et al.* 2005); similar studies on the bryophyte diaspore bank are lacking. Our data showed that the bryophyte diaspore bank was unaffected by grazing intensity. The diaspore bank can maintain its vitality for a very long time as proved by During (2007), so it is quite understandable that the short period of low grazing did not affect its diversity. Bryophytes can germinate from spores or from various vegetative propagules. In our study, 35 bryophyte species germinated from the diaspore bank. The diaspore bank contained equal numbers of acrocarpous and pleurocarpous species, but more pleurocarpous species were found above ground. This was also found in other grasslands (During & ter Horst 1983, During *et al.* 1987, van Tooren *et al.* 1990). The diaspore bank plays different roles depending on the characteristics of the life history and environment of each species. The diaspore bank of annual bryophytes often serves the same purpose as the seed bank for annual vascular plants, enabling the species to germinate in favourable conditions and evade unfavourable ones (During 1997). Diaspore banks may also serve as accumulators of genetic variability over generations (Hock *et al.* 2008). Longevity of several bryophyte diaspores was shown by During (2001, 2007), but it remains unknown how long the composition and richness of diaspore banks in meadows are maintained after cessation of grazing. Our study showed that grazing intensity does not affect composition or richness of the bryophyte diaspore bank in the Baltic coastal meadows, at least during short periods, but since low grazing intensity inhibits germination, this might over longer periods lead to impoverishment of the whole local bryophyte species pool. The unexpectedly diverse diaspore bank in these coastal meadows makes them intriguing for more detailed studies in the future.

We conclude that grazing intensity and amount of litter in coastal meadows have a different effect on the species richness of bryophytes and vascular plants, respectively. The richness of the bryophyte diaspore bank, which in this study included more than two thirds of the local bryoflora in coastal meadows, is unaffected by grazing intensity.

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