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Change in species composition during 55 years: a re-sampling study of species-rich meadows in Estonia

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We revisited 44 remnants of historically species-rich meadows in two regions in Estonia in order to evaluate their importance in harbouring meadow species. We used Ellenberg's indicator values (EIV), diversity and evenness indices and species functional traits (CSR strategy, height, clonal mobility, ramet life span) to analyse changes in vegetation and habitat conditions. Habitat loss resulted in similar amount of loss of both meadow specialists and generalists. Only meadow specialists were negatively affected by cessation of management in meadows unmown for more than 10 years in South Estonia. The largest change was an increase in Ellenberg's indicator value (EIV) of nutrients. We found a significant decline in typical meadow species (e.g. *Briza media*, *Primula farinosa*) and an increase in strong competitors. Species in the remnant meadows tended to have increased clonal mobility and shortened ramet life span, indicating fertile habitats. The ecological conditions became unfavourable for meadow species which prefer high illumination and unfertile conditions. The remnant meadows have largely lost the floristic diversity of the original nutrient-poor or moist species-rich meadows.

Introduction

The high rate of human-induced conversion makes meadows one of the most endangered habitats in the world (Hoekstra *et al*. 2005). Most current meadows are either mere remnant patches of larger meadows or newly established and successionally young habitats. The area of meadows in various European countries declined during the last 100–200 years by as much as 90% (Poschlod & WallisDeVries 2002, Luoto *et al*. 2003, Adriaens *et al*. 2006, Cousins *et al*. 2007, Sammul *et al*. 2008a, Zomeni *et al*. 2008, Waesch & Becker 2009). This decline can be attributed to abandonment, afforestation and conversion of meadows into arable land (Smart *et al*. 2005, Tamis *et al*. 2005, Walker *et al*. 2009). Degradation of habitat quality and loss of habitat area lead to declines in species richness (Hansson & Fogelfors 2000, Pykälä *et al*. 2005, Marini *et al*. 2008, Walker *et al*. 2009, Dahlström *et al*. 2010, Lindborg *et al*. 2012). The intrinsic value of a meadow (species richness, high concentration of rare species, etc.) is largely a function of continuity, i.e. age (Kukk & Kull 1997, Austrheim & Olsson 1999, Pärtel *et* *al*. 2005a, Aavik *et al*. 2008, Waesch & Becker 2009) and size (MacArthur & Wilson 1967, Rosenzweig 1995). Although some small remnant meadows may still be speciose, it may be merely a transient legacy from earlier periods (Helm *et al*. 2006).

Species are expected to differ in their sensitivity to habitat decline, but those differences remain largely speculative. A study on the effect of the decline of calcareous grasslands has shown a decrease or disappearance of plants with good dispersal ability, shorter life span, non-clonal growth, self-pollination, fewer seeds per shoot, and lower average height (Saar *et al*. 2012). Marini *et al*. (2012) found that species with high competitive ability, annual life cycle and dispersal by animals coped better with habitat decline. Lindborg *et al*. (2012) found that forest species are more vulnerable to area loss than grassland species. Among grassland species, clonal and long-lived species were more affected by a decline in habitat area than non-clonal plants.

Abandonment of meadows changes the environmental conditions in the remnant patches (Schleuning & Matthies 2009). These changes usually result in higher rates of competitive exclusion of species (Jacquemyn *et al*. 2003, Rajaniemi *et al*. 2003, Ehrlén *et al*. 2005) as an increase in productivity (Mitlacher *et al*. 2002) leads to the dominance of few species (Öckinger *et al*. 2006, Marriott 2009, Dahlström *et al*. 2010, Pakeman & Marriott 2010). Tall grasses and shade-tolerant forbs usually increase in abundance (Kahmen & Poschlod 2004, Pavlů *et al*. 2005), which intensifies competition for light. Hence, light-demanding species probably decline most in abandoned meadows. It has been shown that the less competitive species (Ryser *et al*. 1995) can in fact be meadow specialists (Pywell *et al*. 2003).

Historical data sets provide the means to analyse vegetation change and forecast future development (Kuussaari *et al*. 2009, Wesche *et al*. 2012). However, the scarcity of appropriate historical data limited a number of studies comparing past and present vegetation. Some studies addressed the effects of intensive agriculture on savannas, calcareous grasslands and general landscapes (including various grasslands, swamps, heaths, mires, etc.; Fischer & Stöcklin 1997, Sutton & Morgan 2009, Walker *et al*. 2009, Saar *et al*. 2012). Long-term floristic changes have resulted from an increase in nutrient-rich habitats (also intensively managed grasslands) (Van der Veken *et al*. 2004, Tamis *et al*. 2005, Sammul *et al*. 2008a) and from a decline in grassland specialists, stress-tolerators in grassland communities (McCollin *et al*. 2000, Walker 2009).

Temporal continuity and continuous low-intensity management are the most important factors in preserving high biodiversity in Estonian meadows (Pärtel *et al*. 2005b, Aavik *et al*. 2008, Sammul *et al*. 2008b). Nevertheless, the temporal continuity of grasslands is low (Kana *et al*. 2008) and the amount of agricultural land in the eastern Estonia has increased during the 20th century (Palang 1994). In this study, we compared the historical and existing floristic composition and species richness of species-rich meadows and their current remnants. This approach enabled us to associate ecological changes in historical meadows with ensuing changes in species composition. We aimed to identify species whose frequency declined and that are likely to suffer from an ongoing degradation and disappearance of meadows. More specifically, we used historical floristic data to test the following hypotheses: (1) the decline of meadow areas has resulted in a decrease in species richness in remnant habitat patches; (2) meadow specialists have decreased more than others due to the degradation of meadows; (3) eutrophication, caused by ceased management, has resulted in more severe competition, in which declining species are weak competitors, having a high demand of light, and being low and less able to spread vegetatively.

Material and methods

Study regions

We studied meadows in two regions, both ca. 500 km^2 in size: one in Central Estonia (58°N, 25°–26°E) and the other in South Estonia (57°–58°N, 26°E). The two regions are separated by about 80 km. The region in Central Estonia is a glacial till plain, conducive to agriculture. The bedrock consists mainly of limestone or marl and the dominant soil types are brown soils and sod-podzolic soils (Kõlli & Lemetti 1999, Arold 2005). The relief in the South Estonia region is slightly hilly. The bedrock consists of sandstone and clay. The main soil type is sod-podzolic (Arold 2005). About 60% of the Central Estonia area is agricultural land and ca. 40% is forested. In the South Estonia region, both agricultural land and forests cover ca. 45%.

Historical vegetation data

We used an historical map of Estonian vegetation to select the meadows for revisitation. The map was published after an extensive study conducted between 1934 and 1956 to classify and map vegetation throughout Estonia. Our selection includes semi-natural meadows, which were classified as fresh species-rich meadows.

All the meadows in our study had originally been mapped and sampled in 1954. The vegetation data for each meadow was collected from its most characteristic area: all vascular plant species and their abundances (on a scale of 1 to 5) were recorded in a randomly-located 2-m^2 plot (Kalda 1953). Sampling effort increased with the size of the meadow, with at least one plot per 0.25 km^2 being sampled. Additional samples were taken in meadows exhibiting dissimilar abiotic (e.g. moister) conditions. Meadows where more than one sample per area was made in 1954 occurred only in Central Estonia (Table 1). The total number of original samples (plots) was 18 in Central and 12 in South Estonia.

Map analysis

The boundaries of meadows in 1954 (henceforth original meadows) were digitised using the scanned 1954 vegetation map and corrected using decoded aerial photographs (ortophoto maps) taken in 1948. The topographic map used to map vegetation in 1954 was published in 1900 and had a scale of 1:42 000 (Laasimer 1965). We analysed the current land cover of the origi-

Table 1. Number and area (ha) of meadows in Central and South Estonia, land cover types in 2009 in the area of former original meadows, and management of the remnants.

Number and area of meadows	Central Estonia	South Estonia
Total number		
Original meadows 1954	10	12
Remnant meadows 2009	23	21
Total area		
Original meadows 1954	1306	223
Remnant meadows 2009	29	29
Mean area		
Original meadows 1954	130.6	18.5
Remnant meadows 2009	1.1	1.6
Current land cover in the area of original meadows (%)		
Forest	62	31
Agricultural land (arable fields, cultivated meadows)	34	55
Meadow remnants	2	14
Other	2	0
Mowing		
Number of meadows		
last mown in 2009 or 1–3 years before	9	5
last mown 4–10 years before	11	3
last mown more than 10 years before	3	13
Share of total area of studied meadows (%)		
last mown in 2009 or 1–3 years before	40	66
last mown 4–10 years before	53	7
last mown more than 10 years before	7	27

* percentage of total original area in 1954, ** percentage of total area of remnants in 2009.

nal meadows by using a basic map of Estonia (1:10 000, from 2002) and contemporary aerial photographs (1:10 000, from 2002). We identified all patches that were still meadows in 2009 (henceforth: remnant meadows). We excluded patches that proved to be formerly arable land or cultivated (i.e. sown) meadows, i.e. those exhibiting clear signs of ploughing.

With the aid of the basic map, we determined the land cover types (forest, arable land, grassland, wetland, scrub, waterbody, settlement area and roads) that supplanted the original meadows. We used the GIS software MapInfo Professional ver. 7.8 (MapInfo Corporation) for all map analyses.

Sampling of remnant meadows

All 44 remnant meadows were revisited in July 2009. In order to assure proper comparisons, we copied the original sampling methods used in 1954 (*see* 'Historical vegetation data'). The most typical part (representative area) of a remnant was chosen for sampling. All plant species in one randomly-located 2-m^2 plot were recorded using the abundance scale of Braun-Blanquet (1964). In addition, a list was compiled of all species growing within ca. 6 m around each plot. These species, when added to the number of species in each plot, make up what is hereafter called a "cumulative species richness" of the representative area.

Mowing was the only form of land management detected in the remnant meadows. The mowing status of the remnants was classified as (1) last mown in 2009 or 1–3 years before; (2) last mown 4–10 years before; (3) last mown > 10 years before. This assessment was done visually, taking into account the amount of litter, presence of turf, presence and abundance of young trees and bushes, as well as information about management history (e.g. time since last mowing) obtained from local inhabitants.

Data analysis

A general linear model (GLM) with the survey time as repeated measures factor and the management status (three classes) as fixed factor was used to analyse changes in meadow size and species richness in 1954–2009. For species richness, the percentage of meadow area that was still present in 2009 compared with the meadow area in 1954 was included in the model as a continuous factor. Repeated measures ANOVA enables to discover if the temporal change in area and/or species richness differs among differently-managed meadows. To test more specifically if differently-managed remnant meadows differ in their size and species richness (general species richness, meadow specialists and other species) per plot, we used one-way ANOVA with management as categorical factor. The weighted averages of Ellenberg indicator values (EIVs) and plant height, clonal mobility (mm year^{-1}) and ramet life span (years) in the original meadows and their remnants in 2009 were tested by repeated measures ANOVA to unravel changes in those traits, as they are related to competitiveness and persistence (Herben *et al*. 1994, Adriaens *et al*. 2006). In this and in all other analyses, species abundance was used as weight of weighted averages. The height was obtained from Leht (2007) and the data on clonal growth from the database of clonal plants of Estonian meadows (Sammul *et al*. 2003, Klimešová *et al*. 2011, Sammul 2011). The data from the two regions were analysed separately to reduce the chance of region factor to mask the effect of other factors. Means were compared with the unequal *N* HSD *post-hoc* test.

Relationships between species richness in plots (general richness, meadow specialists and other species) and meadow area in 1954 and 2009 were tested by regression analysis.

Detrended Correspondence Analysis (DCA) was used to compare the species composition of original and remnant meadows. The abundance of species in plots was used in a data table consisting of 74 samples. The weighted averages of the EIVs for light, moisture, soil reaction and nutrients (Ellenberg 1974, Ellenberg *et al*. 1992) were used as proxies for environmental attributes to interpret the results of ordination analysis. Relations between the EIVs, Shannon-Weaver's diversity and evenness indices and the values of the DCA axes for the respective meadow were tested using Pearson's correlation analysis.

The floristic turnover in each meadow was described using the following groups: (i) the per-

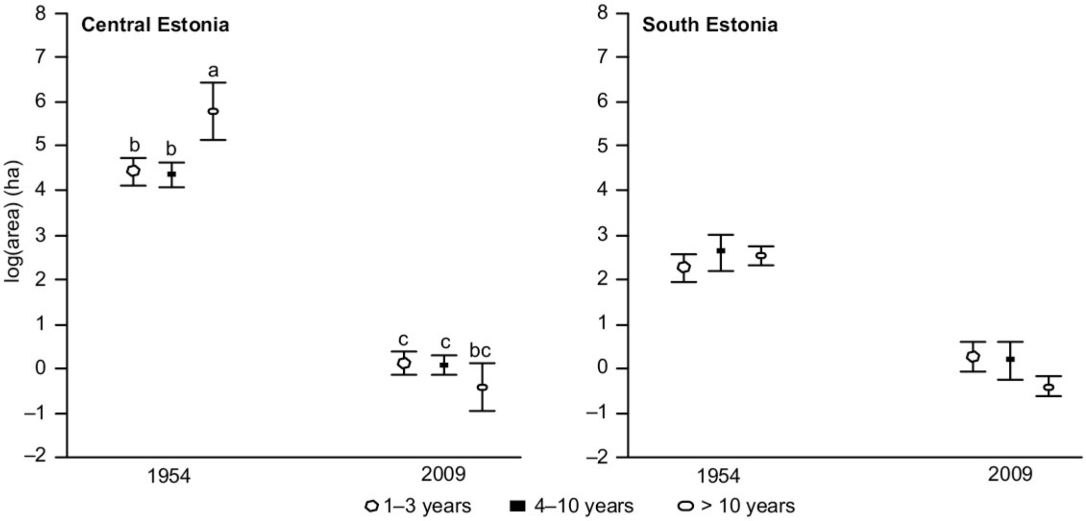

Fig. 1. Areas ± SE of meadows mown 1–3 years, 4–10 years or more than 10 years earlier in Central and South Estonia. Different letters above the error bars indicate significant differences (unequal *N* HSD *post-hoc* test) and are shown when the interaction between time and management was statistically significant ($p < 0.05$).

centage of persisting species, (ii) species present only in the 1954 survey, i.e. "lost species" and (iii) species present only in 2009, "new species". The species list of the representative area was used for remnants. To reveal the dynamics of species with different habitat preferences, we divided the species into two groups: meadow specialists and other species representing generalists or species typically found in other habitats. This distinction was made using the database of the habitat preferences of Estonian species (*see* Sammul *et al*. 2008a).

The significance of changes in species frequency (percentage of original meadows and remnants occupied by a species) was tested with the exact alternative (Liddell 1983) of the McNemar test (McNemar 1947), which uses exact binomial probability calculations and is a special case of the sign test. This method is suitable for analysing very small frequencies (incl. zero counts) and it takes into account that during the two surveys (1954, 2009) the same meadows were visited and, thus, the samples are not independent. The frequency in 2009 was based on the presence in the plot and in the representative area.

We compared the following species traits among the groups of decreasing and increasing species: type of CSR strategy (abbreviation from the words Competitive, Stress tolerant, Ruderal; Grime 1979), average height, clonal mobility and ramet life span. Data on the strategy of species was taken from the database BiolFlor (Kühn *et al*. 2004). Averages of all numerical traits were compared using a Mann-Whitney *U*-test.

The values of Shannon-Weaver's diversity and evenness indices were calculated using PC-ORD 4.0 (McCune & Mefford 1999), DCA from CANOCO 5.0 (ter Braak & Šmilauer 2002). Other statistical analyses were performed with STATISTICA ver. 8 (StatSoft Inc.).

Results

Size and management of meadows

GLM showed that meadows had significantly declined between 1954 and 2009 in both Central Estonia ($F_{1,20} = 59.8$, $p < 0.0001$) and South Estonia ($F_{1,18} = 14.3$, $p = 0.001$; Fig. 1). In Central Estonia also the main effect of management status ($F_{2,20} = 5.9$, $p = 0.01$) and its interaction with time ($F_{2,20} = 6.1$, $p = 0.009$) were significant. In the same area, the long-term unmown meadows were historically nearly three times larger than other meadows and they had undergone the greatest decline in size between 1954

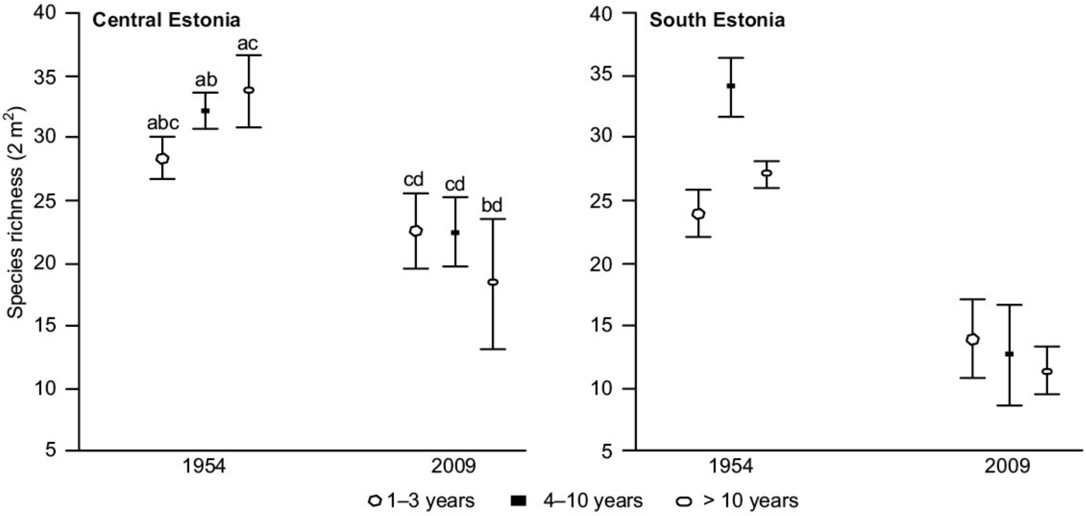

Fig. 2. Species richness ± SE per 2 m^2 in meadows mown 1–3 years, 4–10 years or more than 10 years earlier in Central and South Estonia (*see* legend of Fig. 1). Different letters above the error bars indicate significant differences (unequal *N* HSD *post-hoc* test) and are shown when the interaction between time and management was statistically significant ($p < 0.05$).

and 2009. The large difference in total area between original meadows in Central Estonia and South Estonia in 1954 no longer existed in 2009 (Table 1).

Several species-rich meadows were entirely lost during the period between the two surveys: 33 in Central Estonia (3911 ha) and 28 in South Estonia (425 ha). These losses in Central Estonia were largely due to overgrowing and afforestation, whereas replacement by agricultural land (i.e. arable fields and cultivated grasslands) was the main cause in South Estonia (Table 1). In Central Estonia > 80% of the remnants had been mown within the last ten years, whereas in South Estonia > 60% of the remaining meadows had been abandoned for more than ten years (Table 1). The size in 2009 did not differ among the meadows with different mowing status in either region; mean values varied between 0.5 and 1.5 ha in Central Estonia and between 1.3 and 1.5 in South Estonia.

Species richness and composition

GLM showed a significant change ($F_{1,14} = 7.06$, $p = 0.019$) in species richness per plot in South Estonia (Fig. 2), while management status and percentage of meadow area that persisted in 2009 did not differ. In Central Estonia, the effect of time was significant ($F_{1,17} = 7.78$, $p = 0.013$) as well as the interaction between time and management status ($F_{1,17} = 3.70$, $p = 0.046$). The interaction between the three factors remained marginally insignificant ($F_{1,17} = 3.47$, $p < 0.054$). In 1954, the species richness per plot in the two regions was rather similar, but by 2009 the remnants in South Estonia experienced steeper loss of diversity than the remnants in Central Estonia.

Total species richness in 2009 showed a slight decrease in long-term unmown meadows in both regions, but the decline was statistically insignificant. Management status had a significant effect only on the species richness of meadow specialists in South Estonia ($F_{2,17} = 4.08$, $p = 0.036$). Both the total species richness ($r = 0.53$, $F_{1,42} = 16.96$, $p = 0.0002$) and the richness of meadow specialists ($r = 0.50$, $F_{1,42} = 13.92$, $p = 0.0006$) in 2-m^2 plots in 2009 were related positively to the original area of meadows, but only when the data from the two regions were analysed together. The present meadow area was unrelated to total species richness, richness of meadow specialists or generalists.

Significant ($p < 0.05$) temporal changes occurred in all studied plant traits in meadows in both regions: height and clonal mobility increased, and ramet life span decreased. The changes were more pronounced in South Estonia, particularly in height (increase from 46.3 to 62.3 cm) and clonal mobility (increase from 21.6 to 54.6 mm year^{-1}). A significant decrease in EIV of light and increase in EIV of nutrients occurred in both regions ($p < 0.05$). EIV of light decreased from 6.9 to 6.6 in South Estonia and from 7.1 to 6.7 in Central Estonia. EIV of nutrients increased from 3.8 to 6.0 in South Estonia and from 3.2 to 4.9 in Central Estonia. No significant changes were found for EIVs of moisture. EIV of reaction decreased significantly only in Central Estonia ($F_{1,22} = 8.16$, $p = 0.009$), from 6.6 to 6.1. Accordingly, the most substantial change in ecological conditions was related to the EIV of nutrients.

Species composition changed significantly between 1954 and 2009. In general, the number of persistent species was slightly greater in Central Estonia (30%) than in South Estonia (20%). The percentage of meadow species decreased (Fig. 3), especially in South Estonia. Most species in the remnants were not present in their original meadows (Fig. 4). DCA revealed a considerable difference in species composition in original meadows and remnants in both regions (Fig. 5). The original meadows in the regions formed two homogeneous and distinct groups. The remnant meadows varied floristically more than the original meadows, with some overlap between the regions. The eigenvalues of the first and second axis were 0.56 and 0.36, respectively. The first axis correlated with light, nutrients, species richness, evenness and diversity, and the second axis with light, nutrients and evenness (Table 2).

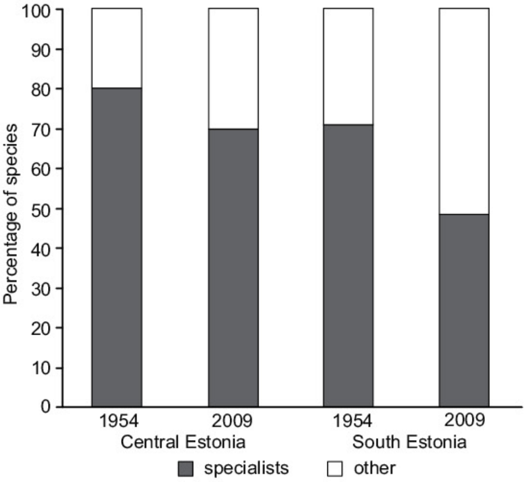

Fig. 3. Proportions of meadow specialists and species of other habitats in original meadows (1954) and remnants (2009) in Central and South Estonia. Based on 2-m^2 plots.

Dynamics of species

Frequency of occurrence of 19 species in Central Estonia and 15 in South Estonia changed significantly ($p < 0.05$) (Table 3). Among the declining species, two in Central Estonia (*Primula farinosa*, *Polygala amarella*) and two in South Estonia (*Briza media*, *Trifolium pratense*) were not found in any remnants. In addition, there were 19 species in Central Estonia and 28 in South Estonia which occurred in fewer than six meadows in 1954, and were not found at all in 2009. Due to such a small number of occurrences in 1954 and the relatively conservative statistical method used, their disappearance was statistically not significant and those species were omitted from further analysis of traits of declining species. The dominant strategy type among the decreasing species was CSR (10 species, 70%), whereas the increasing species were mostly C species (11 species, 55% of the species whose frequency had increased significantly). The increasing species were significantly taller ($U = 54.5$, $Z = 2.0$, $p = 0.045$), more nutrient-demanding ($U = 13$, $Z = 3.12$, $p = 0.002$) and less moisture-demanding ($U = 16$, $Z = -2.73$, $p = 0.006$) than the decreasing species. We found no significant differences between ramet life span and clonal mobility in increasing or decreasing species.

Discussion

Land use change has caused a drastic loss of species-rich meadows in Estonia during the last 55 years: only small patches of former meadows still exist in both study regions. The loss of more than 90% of meadow area is similar to the decline of meadows in other parts of Europe (Hansson & Fogelfors 2000, Lennartsson *et al.*

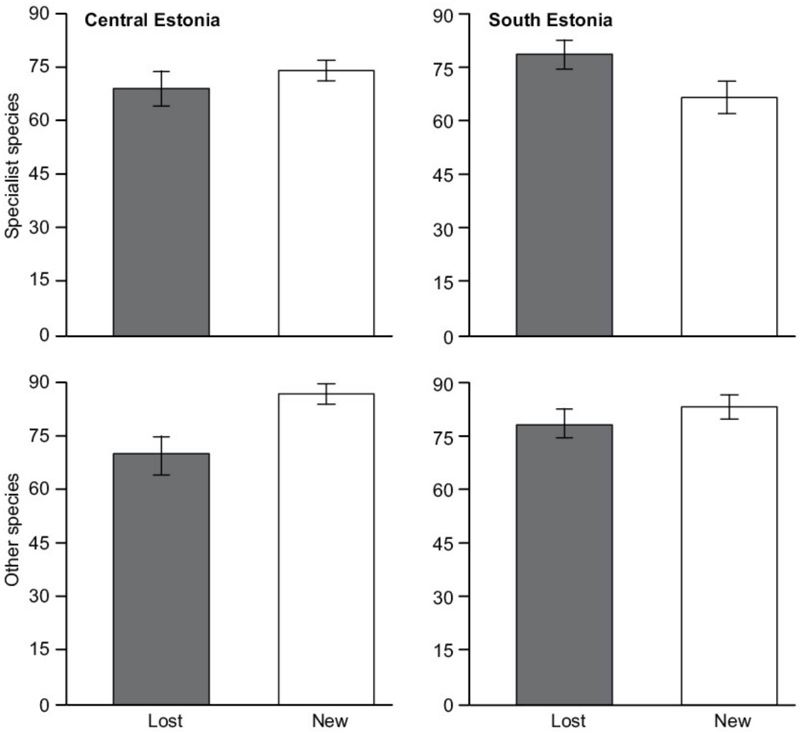

Fig. 4. Mean ± SE proportions (%) of lost and "new" (i.e. not present in 1954) species. Proportions were calculated taking into account species richness of representative areas in 2009.

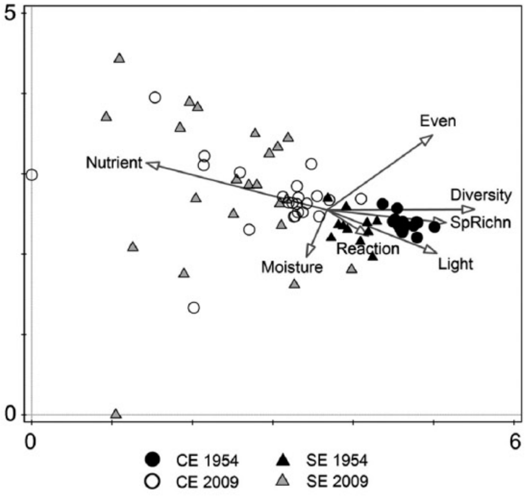

Fig. 5. Meadows in Central Estonia (CE) and South Estonia (SE) in 1954 and 2009 on the DCA plot. The vectors illustrate the correlations between average Ellenberg indicator values, diversity index and evenness (Even) index with the first and second axes.

2012). A significant decline in meadow area occurred in both studied regions. Meadows in South Estonia were mostly replaced by agricultural land, whereas the once large meadows in Central Estonia are largely overgrown with forest. In South Estonia, the differently managed meadows did not differ in their historic size while in Central Estonia the meadows unmown for a long time were once much larger than others. No size differences were found among groups of differently managed remnants in South Estonia or Central Estonia.

Surprisingly, the major loss in meadow area in Central Estonia was not accompanied by proportional decline in species richness as in South Estonia, where a smaller decline in habitat size has taken place. The greatest decline in size had occurred in meadows unmown for a long time in Central Estonia, which were historically large and the most species-rich. Their diversity has decreased to the lowest value in the region but remained higher than that in South Estonia. The cumulative effect of various factors could explain the greater decline in species richness in South Estonia. Firstly, the South Estonia meadows were converted largely into arable fields, which led to an immediate loss of suitable habitat around the remnant. Secondly, the survey in

1954 could have overlooked the high within-habitat diversity of the larger meadows. The original meadows in Central Estonia, being ten times the size of those in South Estonia, could have been more species-rich on the community level, despite being reciprocally species-rich at the plot scale. Hence, the difference in species richness of remnants could be attributed to differences in the size of their historical species pools and to the character and speed of habitat loss. This explanation is supported by the finding that the current species richness is related to the historical area, not to the current meadow area, an obervation that has been made in previous studies elsewhere (Helm *et al.* 2006, Cousins *et al.* 2007). Thirdly, in most remnants in South Estonia mowing was ceased, which led to higher sward, intensified competition and decreased diversity.

As the percentages of lost species per original meadow were similar for meadow specialists and other species within the regions, species of either group had a similar probability to disappear with habitat loss (sampling effect *sensu* Gonzalez 2000). The loss of original species was smaller in Central Estonia (70%) than in South Estonia (77%). Species of other habitats and generalist species increased their numbers in South Estonia as the ecological conditions of the remnants became more suitable for them. This improvement in conditions could have resulted from inconsistent mowing. Most remnants in Central Estonia were mown within the last ten years, whereas mowing in South Estonia was

Table 2. Correlation coeficcients between DCA ordination axes scores and Ellenberg indicator values (EIVs; light, moisture, reaction, nutrients), species richness, evenness, and diversity. * $p < 0.05$, ** $p < 0.002$, *** $p < 0.001$.

	Light	Moisture	Reaction	Nutrients	Species richness	Evenness	Diversity
Axis 1	0.3914**	–0.1923	0.1033	–0.8097***	0.7020***	0.3870**	0.7521***
Axis 2	–0.3223*	–0.1457	–0.1799	0.3842**	–0.1963	0.4094***	–0.0642

Table 3. Species whose frequency (number of occupied meadows in 1954 and 2009) changed significantly (*p* values from the McNemar test).

Central Estonia				South Estonia			
Species	1954	2009	*p*	Species	1954	2009	*p*
Decreased frequency				**Decreased frequency**			
Briza media	10	4	0.04	*Anthoxanthum odoratum*	9	1	0.01
Polygala amarella	6	0	0.04	*Briza media*	11	0	0.003
Primula farinosa	6	0	0.04	*Carex caespitosa*	10	3	0.02
Scorzonera humilis	9	3	0.04	*Carex panicea*	12	3	0.007
Sesleria caerulea	10	2	0.01	*Galium uliginosum*	10	3	0.02
Increased frequency				*Trifolium pratense*	7	0	0.02
Achillea millefolium	1	8	0.045	**Increased frequency**			
Agrostis stolonifera	0	6	0.04	*Agrostis capillaris*	0	8	0.01
Alopecurus pratensis	0	7	0.02	*Anthriscus sylvestris*	0	11	0.003
Anthriscus sylvestris	0	7	0.02	*Cirsium arvense*	0	9	0.007
Elymus repens	0	6	0.04	*Dactylis glomerata*	2	9	0.02
Festuca rubra	0	10	0.004	*Elymus repens*	0	6	0.04
Galium uliginosum	0	6	0.04	*Galium album*	0	9	0.007
Helictotrichon pratense	2	8	0.04	*Lysimachia vulgaris*	0	6	0.04
Helictotrichon pubescens	0	7	0.02	*Poa angustifolia*	0	6	0.04
Lathyrus pratensis	1	9	0.01	*Urtica dioica*	0	7	0.02
Phleum pratense	0	8	0.01				
Poa angustifolia	0	7	0.02				
Poa pratensis	1	9	0.01				
Veronica chamaedrys	0	9	0.008				

much more irregular. A trend of decline in total species richness appeared in unmown meadows in both regions, but the effect of management status remained insignificant. However, significantly lower number of species of meadow specialists occurred in meadows unmown for a long time in South Estonia. We conclude that the temporal decline in species richness is mainly explained by habitat loss, but a decline in species richness due to management change is also taking place. Continued degradation of unmown meadows is evident and hence their potential to support and to disperse meadow specialists in the landscape will likely continue to decline.

In both study regions eutrophication has changed the vegetation of meadows. We revealed an increase in sward height and in abundance of C strategists in the remnants. Clonal mobility and ramet life span have increased, which support the findings of a fertilisation experiment in an Estonian wooded meadow (Sammul *et al.* 2003). Many of the increasing species (e.g. *Dactylis glomerata*, *Elymus repens*, *Aegopodium podagraria*, *Urtica dioica*) are characteristic of highly fertile habitats. Eutrophication causes remnant meadows to become more competition-driven, which has likely led to the floristic similarity of the two regions (*see* section 'Species richness and composition' for ordination results). Increase in soil fertility could be caused by local processes, such as cessation of mowing and agricultural cultivation in the neighbourhood, as well as an increased atmospheric nitrogen deposition. Nitrogen deposition is a widespread threat to nutrient-poor habitats (Bobbink *et al.* 1998, Stevens *et al.* 2011).

None of the declining species in our study are currently in the threatened categories of the Estonian Red List, but several have been reported as declining in other countries. *Primula farinosa* has decreased throughout Estonia (Kukk & Kull 2005) and is vanishing widely from Europe (Hambler & Dixon 2003, Lienert & Fischer 2003, Toräng & Vanhoenacker 2009). A decline of *Scorzonera humilis* in Europe has likewise been reported (Wigginton 1999, Colling *et al.* 2002). *Briza media* was the only species whose frequency declined significantly in both studied regions. Some decreasing species are characteristic of moist, species-rich meadows (e.g. *Carex caespitosa*, *C. davalliana*, *C. panicea*, *Galium uliginosum*, *Primula farinosa*), some of nutrient-poor meadows (*Anthoxanthum odoratum*, *Briza media*, *Polygala amarella*, *Scorzonera humilis*, *Sesleria caerulea*).

Hence, well-preserved remnants of these meadow types need to be maintained carefully and their regular management should be prioritized.

Conclusions

The decline of meadows and changes in their ecological conditions have resulted in a drastic change in the initial habitat distribution and species composition. The latter change appears to be a result of the combined effect of habitat loss and irregular management leading to increased soil fertility. The latter explains well the decrease and increase of particular species. Declining species, which are weak competitors and prefer nutrient-poor conditions, were replaced in remnant meadows by strong competitors. These changes reveal that remnant meadows do not function as centers of meadow-specific floristic diversity, particularly in South Estonia.

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