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Effects of reforestation and intensified land use on vascular plant species richness in traditionally managed hay meadows

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In this study of 130 sites with different management we investigated whether vascular plant species richness is significantly reduced when traditionally managed hay meadows are abandoned and reforested. We also compared the effects of reforestation with those of intensified land-use to see which have the largest effects on species richness. Finally, we investigated the relative importance of relevant ecological factors for species richness. While the use of artificial fertilizers in traditionally managed hay meadows has resulted in significantly lower species richness, and intensive cultivation in even lower species richness, abandonment with reforestation has not decreased the species richness significantly. Productivity and habitat diversity have determined the species richness of meadows on the scale (0.03–5.1 ha) of this study. Low productivity is a prerequisite for high species richness in meadows. Maximum species richness was observed in unproductive, old, traditionally managed hay meadows with a high soil pH and high habitat diversity. The high species richness of these meadows suggests that they are in urgent need of conservation.

Key words: agricultural landscapes, hay meadows, reforestation, species-area curves, species richness

Introduction

At scales between 0.001 and 10 m^2, the most species-rich vascular plant communities in the world are temperate grasslands (Peet *et al.* 1983, Walker & Peet 1983, Shmida & Ellner 1984, Grubb 1986, Willems *et al.* 1993, Klimes 1999), and particularly nutrient-poor calcareous grasslands (Zoller 1954, Zoller & Bischhof 1980, Willems 1982, 1990, Ellenberg 1988, Kull & Zobel 1991, Fischer & Stöcklin 1997, Poschlod *et al.* 1998). These are often considered as "hot spots" for biological conservation. Traditionally managed pastures and hay meadows in Norway are species-rich (Losvik 1993, Norderhaug 1988, 1996) and contain a number of species that are threatened or vulnerable to extinction due to agricultural intensification or

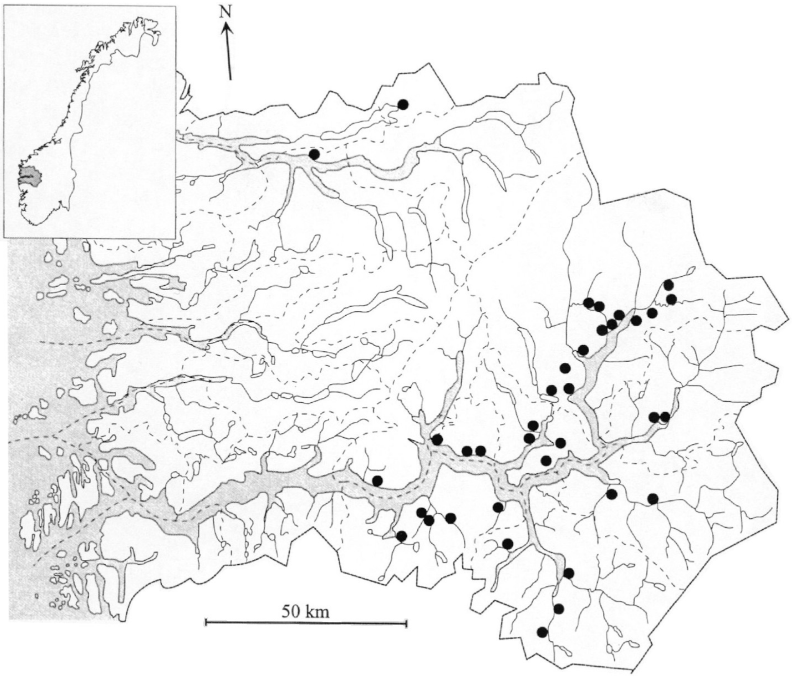

Fig. 1. Map of Sogn og Fjordane county, western Norway, showing the distribution of the 130 sites surveyed. Many of the sites are so close that they cannot be shown seperately. Therefore only 36 dots are marked on the map.

abandonment (Høiland 1996). However, these once wide-spread communities are now rare and rapidly disappearing largely due to changes in land-use practises including intensification (use of artificial fertilizers, frequent ploughing and reseeding; Willems 1982, Hughes & Huntley 1988, Fisher & Stöcklin 1997, van Andel 1998) and abandonment (Ellenberg 1988, Lavorel *et al.* 1998). These are both likely to threaten biodiversity in semi-natural sites (Ostermann 1998).

The present study is a regional survey of 130 sites localised in the county of Sogn og Fjordane, western Norway. The following land-use types were studied: traditionally managed hay meadows (defined as more than 50 years old and never artificially fertilized hay meadows, some lightly fertilized with dung only, hereafter termed traditional meadows); lightly fertilized meadows, artificially fertilized hay meadows (defined as old, artificially fertilized hay meadows, hereafter termed artificially fertilized meadows); intensively cultivated grasslands (defined as less than 10 years since ploughing and heavily fertilized grasslands) and abandoned and reforested traditional meadows (hereafter termed reforested meadows). Vascular plant species richness of traditional meadows was compared with that of artificially fertilized meadows, intensively cultivated grasslands and reforested meadows, and we had two main questions:

1. Which management changes result in the greatest species losses locally? Specifically we aimed at detecting whether or not species richness will become significantly reduced when traditional meadows are abandoned and reforested, and further, at comparing the effects of reforestation with the effects of different degrees of land use intensification to see which has the most negative effects on local species richness. Species richness is known to decrease with reforestation of meadows when using small sampling squares (1 m^2) (Zobel *et al.* 1996, Einarson & Milberg 1999), however no decrease was found using larger sampling quadrats (5 × 20 m) (Milberg 1995). Therefore, in order to be able to compare species richness of meadows with reforested meadows, larger sites of meadows and reforested meadows (0.03–5.1 ha) were sampled by means of species lists rather than a quadrat-based approach in our study.
2. Given a number of meadows, which ones should be conserved and what characterizes

them? Ecological studies which help us to understand the biological processes on farmland may be useful for developing a more targeted environmental policy, trying to avoid the danger that environmental objectives will be misused to provide financial support to farms that are of intrinsically low biodiversity (Bignal 1998). At the time of our survey, none of the investigated high-diversity farms received any financial support, while several of the low-diversity farms were supported. Several factors are known to affect species richness of meadows, among these productivity and disturbance (e.g. Grime 1973, 1979, Huston 1994), habitat diversity (e.g. Huston 1994), area (e.g. Preston 1960, 1962), age (e.g. Gibson & Brown 1992), and soil pH (e.g. Kull & Zobel 1991, Zobel 1992). In this paper we aim to check the relative importance of these and other possible predictors for the species richness of meadows. We had a full productivity gradient from unproductive to highly productive grasslands. Also site mean Ellenberg indicator values for soil moisture, light regime, temperatures and soil nitrogen status were tested as potential predictors, as these indicators have been confirmed by field measurements (Diekmann 1995, Hill & Carey 1997, Schaffers & Sykora 2000, *see* also Dupré & Diekmann 1998) and were successfully repredicted in a study in Britain (Hill *et al*. 2000), showing that their use may be extended outside central Europe. We also wanted to investigate if species-rich meadows tend to have higher occurrences of regionally rare species and higher occurrences of species with narrow ecological tolerances than species-poor meadows.

Material and methods

Data collection

Species data

The field survey was conducted on 130 sites, localised within an area of ca. 78 km × 133 km (approximately 61–62°N, 6–8°E), in the county of Sogn og Fjordane, western Norway during the summers of 1994–1999 (Fig. 1). Species lists of all vascular plants (356 species + 5 species aggregates, a total of 361 taxa, presence/absence data) observed within the 130 sites differing in size (0.03–5.1 ha) were recorded. The frequencies of each taxon within the five management types are given in the Appendix. The 130 sites were chosen so as to represent the total variation in the meadow communities within the region. The number of sites within the 5 different land-use types (A–E below) were: 73 hay meadows (land-use types A–C), i.e. old (not cultivated for 72 years on average), mown once in summer (usually July), usually lightly grazed by sheep a few weeks in spring and autumn, three categories with increasing fertilizer influence (Table 1):

Table 1. Types of management investigated. The number of sites for each management type is given in brackets. Number of species recorded, estimated amounts of fertilizer applied (kg ha^{-1} of: nitrogen = N/ha, phosphorous = P/ha, potassium = K/ha from artificial fertilizer or dung), age (number of years since last ploughing), and area of the sites within the various management types.

Management type	Artificial fertilizer	Number of species	N/ha	P/ha	K/ha	Age (years)	Area (ha)
A: Traditional meadows (21)	Never, small amounts of dung only	37–139	0–7.4	0–5.6	0–21.5	50–over 120	0.03–2.74
B: Lightly fertilized meadows (30)	Small amounts or no artificial fertilizer	26–107	0–21.9	0–9	0–40	26–120	0.05–2.0
C: Artificially fertilized meadows (22)	Moderate amounts	32–89	25–109	0–73	0–250	29–100	0.1–1.91
D: Intensively cultivated grasslands (28)	Heavily fertilized, artificial fertilizer or slurry	8–44	21–332	6–60	19–479	< 10	0.08–5.1
E: Reforested meadows (29)	Never	34–122	Not known	Not known	Not known	Not known	0.05–3.81

A: Traditional meadows (N = 21), i.e. never artificially fertilized, but some very lightly fertilized with dung only, not cultivated for the last 50 years.

B: Lightly fertilized meadows (N = 30) of the following types: (a) artificially fertilized with unfertilized (traditionally managed) edges; (b) lightly artificially fertilized at present; (c) traditionally managed (unfertilized), but younger (26–50 years old) and productive; (d) unfertilized at present, but where we had less information about fertilizer treatement in the past and some may have been traditionally managed.

C: Artificially fertilized meadows (N = 22), higher fertilizer levels than in B category.

D: Intensively cultivated grasslands (N = 28), i.e. mown grasslands ploughed and reseeded with mixtures of fast-growing cultivars of grasses usually every five years, heavily fertilized with manure and/or artificial fertilizer, mown twice in summer for silage production.

E: Reforested meadows (N = 29), some may have been pastures.

Nomenclature of vascular plants follows Lid and Lid (1994).

Possible predictors of species richness

Management as described by farmers (Table 1): Grazing, number of years since ploughing (age of meadow) and mowing. Amounts (kg ha^{-1}) of nitrogen (N), phosphorous (P) and potassium (K) were estimated from the amount of dung applied (never artificially fertilized meadows) or from artificial fertilizer applied by the farmer, using tables from Norsk Hydro (1999).

Site mean Ellenberg indicator values were calculated for nitrogen, light, moisture and temperatures by taking a simple mean over all species in each of the 130 sampled sites, using the Ellenberg indicator values in Ellenberg *et al.* (1991).

Site variables recorded for meadows and reforested meadows: (i) Habitats: stream, stony area, unshaded bare rock, shaded bare rock, presence of trees in meadows and of open sites in reforested meadows; (ii) Habitat diversity = number of habitats recorded; (iii) Percentage surrounding area with meadow and woodland vegetation, slope, altitude, geographical position along a south-north gradient and along a west-east gradient.

Ten soil samples were taken within different parts of each meadow and reforested meadow sampled, and soil pH measured. Total soil carbon and nitrogen were measured from one soil sample for each meadow at the Agricultural Centre for Analysis, Ås, Norway, following international standards (Krogstad 1992), and C:N ratios were calculated.

Numerical analyses

Species-area curves: We calculated the regression slope (z) and intercept (c) using the natural log-log transformation of $S = cA^z$ (Arrhenius 1921, Connor & McCoy 1979), where S is the expected number of species found in area A, z is the rate by which species richness increases with an increase in area, and c is the expected number of species in a unit area. One species-area curve was made for each of the following types of management: traditional meadows, lightly fertilized meadows, artificially fertilized meadows, intensively cultivated grasslands, and reforested meadows.

The tests of the null hypotheses of no statistically significant differences in vascular plant species richness between traditional meadows versus artificially fertilized meadows, intensively cultivated grasslands and reforested meadows respectively, were made using multiple regression of the two types of management to be compared, with management as the predictor dummy variable, and area as a covariable using Redundancy Analysis (ter Braak 1994) as implemented in CANOCO 4.0 (ter Braak and Smilauer 1997) with unrestricted Monte Carlo permutation tests (999 permutations).

The 130 sites were divided into different data sets, so that species richness differences between different types of management could be compared. Multiple regression analyses were carried out using Redundancy Analysis (ter Braak 1994) as implemented in CANOCO 4.0 (ter Braak &

Smilauer 1997) with the effects of area partialled out, choosing the three or four best predictors for differences in species numbers during forward selection permutation tests (ter Braak 1990) (999 unrestricted permutations, all variables with $p < 0.05$ are included). The resulting regression models were tested using Monte Carlo permutation tests (999 unrestricted permutations) and all presented regressions are significant ($p = 0.001$).

Testing the null hypothesis of no difference between measured soil chemical variables between the land-use categories was done using the Mann-Whitney *U*-test choosing a significance level of $p < 0.01$ according to the Bonferroni method of correcting for multiple tests (Cooper 1968).

Do species-rich meadows tend to have more frequent occurrences of species occurring in few sites in our data, than species-poor meadows? Regionally rare species are expected to be found among the species that occur in few sites in our data-set, which is a regional study. Regional frequency of a species was measured by counting the number of sites (out of 130) in which a species was recorded. This was done for all 361 taxa. For each meadow we summed the regional frequencies of all species present and divided this by the number of species present within the meadow. A high value should then indicate many common species in the meadow, whereas a low value should indicate a high content of species with a low frequency in our data-set. Regionally rare species occur among these, however many species have low frequencies for other reasons. This fraction of "rare" species in each meadow was consequently correlated to the number of species recorded in each meadow, using Pearson product moment correlation analysis ($p < 0.01$) (Sokal & Rohlf 1995).

Do species-rich meadows tend to have higher occurrences of species with narrow ecological tolerances than species-poor meadows? The status "indifferent" is the only way in which the Ellenberg system provides information about species tolerances (Ellenberg *et al.* 1991, Schaffers & Sykora 2000). We counted the number of species that were not indifferent to light, temperature, moisture, reaction values and nitrogen in each meadow, and divided this number by the total species number of each meadow, as a measure of the fraction of species with fairly narrow ecological tolerances in each meadow. This fraction was related to the number of species in each meadow using Pearson product moment correlation analysis ($p < 0.01$) (Sokal & Rohlf 1995).

Results

Species-area relationships

The relationship between the number of species recorded in the different management types and areas is shown in Fig. 2, and regression slopes (*z*), intercepts (*c*) and *p* values from the species-area curves are given in Table 2. Intensively cultivated grasslands had the smallest intercept but the largest slope. All the intensively cultivated grasslands consisted of only one habitat and had very low species numbers, including the very large ones. Artificially fertilized meadows had the largest intercept in our data (Table 2).

Traditional meadows and reforested meadows had relatively large intercepts and slopes, thus we found many species in small sites, and many new species as area was increased.

Table 2. Regression slopes (*z*), intercepts (*c*), *p* and R^2 (variance explained) values from the species-area curves of the different land-use types shown in Fig. 2 (number of sites in each type is shown in brackets).

Management type	*c*	*z*	*p*	R^2
A: Traditional meadows (21)	17.05	0.177	0.0005	0.481
B: Lightly fertilized meadows (30)	12.18	0.200	0.0002	0.395
C: Artificially fertilized meadows (22)	34.81	0.056	0.4333	0.031
D: Intensively cultivated grasslands (28)	3.26	0.222	0.0028	0.295
E: Reforested meadows (29)	22.35	0.131	0.0016	0.313

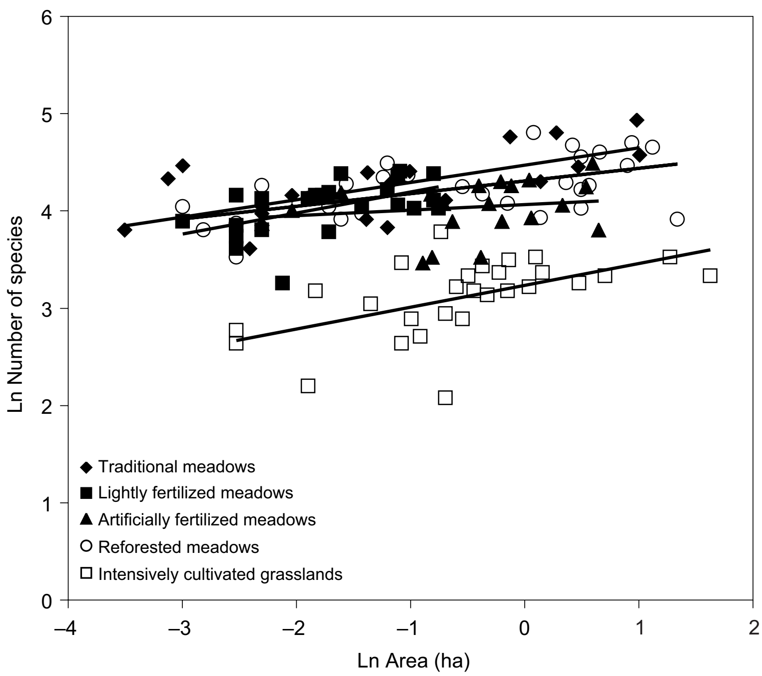

Fig. 2. Species-area curves for the traditional meadows. Regression coefficients are given in Table 2.

Significance tests of species richness differences

Species richness of traditional meadows was found to be significantly higher than species richness of both artificially fertilized meadows ($p = 0.002$, $r = 0.46$, $N = 43$) and species richness of intensively cultivated grasslands when area is controlled for ($p = 0.001$, $r = 0.84$, $N = 49$). Species richness of traditional meadows was, however, not significantly higher than species richness of reforested meadows ($p = 0.22$, $r = 0.17$, $N = 50$). Also, species richness was not significantly higher in traditional meadows than in the lightly fertilized meadows ($p = 0.13$, $r = 0.22$, $N = 51$). Species number of artificially fertilized meadows was significantly higher than the species number of intensively cultivated grasslands ($p = 0.001$, $r = 0.85$, $N = 50$).

Predictors of species richness differences

Habitat diversity and soil pH recorded explained 71.8% of the variation in species richness within the traditional meadows (Table 3, analysis 1). Habitat diversity was strongly correlated to meadow area ($r = 0.76$, $p < 0.0001$). Habitat diversity was still a major predictor of species richness when the effects of area were partialled out, ($r = 0.48$), with habitat diversity and the highest soil pH recorded in the meadows explaining 30.1% ($p < 0.05$) of species richness differences. The most species-rich meadows were very old (at least 120 years old). Age was only weakly correlated to species number ($r = 0.3$ when area was accounted for), even when the effects of variables that may interfere with a correlation between age and species richness (soil pH, habitat diversity and N-fertilizer) had been removed from the analysis.

Species numbers of all meadows (traditional and artificially fertilized, Table 3, analysis 2) constitute a gradient from species-rich traditional meadows with higher habitat diversity and pH-range via less species-rich traditional meadows with low habitat diversity, to species-poor artificially fertilized meadows with higher site mean Ellenberg *N* values. There was a general trend for species richness to decrease when site mean Ellenberg *N* values were above 4 even for meadows that have never been artificially fertilized. Many of the artificially fertilized meadows have higher habitat diversity. However, the number of species was not significantly correlated to habitat diversity for these meadows ($r = 0.45$, $p = 0.07$), whereas these variables were strongly correlated for traditional meadows ($r = 0.77$, $p = 0.0002$). The Mann-Whitney *U*-tests showed no significant differences of measured soil chemical variables (total soil C and N, C:N ratios and soil pH) between meadows with widely different fertilizer treatment (never artificially fertilized as opposed to highly fertilized). C:N ratios and total soil C were significantly correlated with age of meadows ($r = 0.59$, $p < 0.001$ and $r = 0.30$, $p < 0.05$ respectively).

Lower species numbers of intensively cultivated grasslands compared to traditional meadows (Table 3, analysis 3) were correlated to higher site mean Ellenberg *N* values in the intensively cultivated grasslands.

When comparing traditional meadows with reforested meadows (Table 3, analysis 4) a gradient was observed from species-rich traditional meadows and species-rich reforested meadows with higher habitat diversity and soil pH, to species-poor traditional meadows and species-poor reforested meadows. Reforested meadows that do not contain light-exposed bare rock were generally species-poor (Table 3, analysis 5).

Finally, we investigated if species-rich meadows tended to have higher occurrences of species with narrow ecological tolerances and/or higher occurrences of species that are rare in our data than species-poor meadows. Species-rich meadows contained a higher fraction of species with fairly narrow tolerances with respect to light, temperature, moisture, reaction values and nitrogen ($r = 0.51$, $p < 0.0001$, sizes of the fractions ranged from 0.12 in a species-poor meadow to 0.29 in a species-rich).

Species-richness of meadows was also strongly correlated to fraction of species that are regionally rare in our data ($r = 0.87$, $p < 0.0001$). Species that are rare in our data were significantly correlated to meadow age ($r = 0.32$, $p = 0.007$, $r = 0.29$ when amount of N-fertilizer is covariable), while tolerance width was not.

Discussion

Effects of reforestation and intensification on species richness

The comparisons of species richness among the different land-use types suggest that use of artificial fertilizer in traditional meadows has resulted in significantly lower species richness, and intensive cultivation has resulted in very low richness, while species richness of reforested meadows was not significantly lower than spe-

Table 3. Major predictors for differences in species numbers between different management types emerging from 5 regression analyses. The entries of the predictors are in the order of selection. Percentage variance explained of species data by the predictors, their correlation to differences in species numbers, and *t* values of regression coefficients, are shown. The pH variables refer to the lowest, median and range of pH measured from 10 soil samples taken within each meadow.

Analysis	Management	Total variance explained	Predictors	Correlation	*t*
1	A: Traditional meadows *N* = 21	71.8%	Number of habitats	0.78	4.7
			Median pH	0.51	2.7
			Lowest pH	0.15	–1.8
2	A + B + C: All meadows, *N* = 65	43.7%	Number of habitats	–0.50	–2.7
			Potassium applied	0.38	2.3
			Ellenberg *N* values	0.40	2.9
			pH range	–0.29	–2.5
3	A: Traditional meadows + D: intensively cultivated grasslands, *N* = 57	83.0%	Ellenberg *N* values	–0.83	–4.5
			Number of habitats	0.87	6.0
4	A: Traditional meadows + E: reforested meadows *N* = 47	42.7%	Number of habitats	0.60	4.3
			Median pH	0.50	2.8
5	E: Reforested meadows *N* = 26	63.8%	Light–exposed bare rock	0.74	5.9
			Area of rock	–0.25	–2.4

cies richness of traditional meadows. Some of the reforested meadows had high species-richness. High species-richness in reforested as in traditional meadows, was observed in sites with high habitat diversity and soil pH (Table 3, analysis 4). Theoretically, lower species richness due to abandonment would be expected if light-demanding species (large species pool) were replaced by species indicating shade (small species pool) (Zobel *et al.* 1996). Also, light intensity and red/far red ratio is very low under a tree canopy, which partly explains why species number decreases with abandonment, as this is not generally beneficial for germination and survival (Willems 1983). However, in our study the site mean Ellenberg indicator for light regime was not significantly related to differences in species numbers between reforested and traditional meadows, although this indicator was strongly correlated to differences in species composition (Å. Myklestad & M. Sætersdal unpubl. data). Low species numbers were found in reforested sites without bare rock. Thus, abandonment seems to result in lower species richness as a woodland flora replaces the meadow flora, but this is prevented if light-exposed habitats such as bare rock are present. If these open habitats become shaded at a later stage in succession, vascular plant number is expected to decrease. However, although local species richness of traditional meadows may not decrease if they are abandoned and reforested, the meadow flora that was observed in the reforested meadows consisted mainly of generalists, while the habitat specialists observed in the species-rich traditional meadows contributing to regional species richness were absent (Å. Myklestad & M. Sætersdal unpubl. data).

Environmental variability

According to MacArthur (1965; but *see* Connor & McCoy 1979), the intercept parameter in the species-area relationship is a measure of alpha diversity and the slope parameter is a measure of beta diversity. The intensively cultivated grasslands had the smallest intercept but the largest slope in the data set (Fig. 2 and Table 2), suggesting low alpha diversity and high beta diversity. These grasslands may be heterogeneous due to their young age, as different species by chance may grow on the bare, recently ploughed soil, resulting in the possibility of encountering new species with increasing area. The species-area curve for the artificially fertilized meadows, had the largest intercept in our data, but the slope was very small and not significant (Fig. 2 and Table 2). The species-area results thus suggested that the artificially fertilized meadows are rather homogenous, with few occurrences of new species with larger area sampled. Thus, the same species tend to be recorded within different parts of the meadow. The artificially fertilized meadows, in contrast to intensively cultivated grasslands, are old. The tendency for species to reach all micro-sites within a meadow has been described for homogeneous meadows in the 'carousel model' (van der Maarel & Sykes 1993), however these were grazed and nutrient- and water-deficient. Traditional meadows and reforested meadows had relatively large intercepts and slopes (Fig. 2 and Table 2), suggesting both high alpha diversity as well as high beta diversity, thus suggesting that these vegetation types are rather heterogeneous at the spatial scale used in our study. For traditional meadows the increase in species richness with increasing area was related to an increase in habitat diversity, as shown by the multiple regression results. The effects of habitat diversity and area per se on species richness are difficult to separate (Connor & McCoy 1979). However, habitat diversity was significantly correlated to species richness even when the effects of area were partialled out, thus habitat diversity seems to be a major predictor of species richness of traditional meadows. This is in agreement with Huston (1994) in that environmental diversity is one of the strongest correlates of species diversity, as species richness increases with increased number of different habitat types with groups of different species.

Predictors of species richness of hay meadows

One major factor predicting high species richness of hay meadows is the soil nutrient status, shown in this study by the significant decrease in species numbers with use of artificial fertilizer, and by the general trend of species richness decrease when site mean Ellenberg *N* values were above 4 even for meadows that have never been artificially fertilized. Negative effects of fertilization on species richness have been shown in a number of studies (e.g. Mountford *et al.* 1993, Eriksson *et al.* 1995, Mitchley *et al.* 1996, Austrheim *et al.* 1999), while the mechanism(s) by which nutrient additions cause species richness to decline has remained unclear (Willems *et al.* 1993), *see* e.g. Grime (1979) and Leps (1999) versus Tilman (1988), Goldberg *et al.* (1999) and Taylor *et al.* (1990). Meadows with low values of Ellenberg *N* often have nitrophilic species, though in very low cover, in addition to a number of nitrophobic species. Thus the presence of nitrophobic species in a meadow usually means it may be species-rich, while moderate or high cover of one or more nitrophilic species means it is species-poor.

Nutrient-poor meadows were species-rich only if habitat diversity and soil pH was high. Many of the artificially fertilized meadows had higher habitat diversity, yet they were species-poor. Species numbers of traditional meadows were significantly positively correlated to habitat diversity in our study, while species numbers of artificially fertilized meadows were not. Fewer species are expected to occur in different habitats if they are fertilized and thereby productive, as the species pool is predicted to decrease with increasing biomass, while a much wider array of vegetation types exists as fertility decreases and disturbance increases (Keddy & MacLellan 1990). The most species-rich traditional meadows in our data were a mosaic of different unproductive base-rich habitats (up to 5), each adding their particular species. The relationship between high soil pH and high species richness in meadows is in agreement with Ellenberg (1988) and Austrheim *et al.* (1999) and has been explained by a larger species-pool for species present in neutral or base-rich soils (Grubb 1986, Zobel 1992, Bengtsson *et al.* 1994).

Age was not selected as predictor for species richness in the multiple regression analyses, and we were not able to find more than a weak correlation between age and species richness for traditional meadows, thus age seems to be less important for species richness in these meadows than productivity and habitat diversity. However, age is a factor that is very difficult to estimate (e.g. bare rock has never been ploughed, very few farmers know the age of their meadows beyond 50 years, etc.). The most species-rich traditional meadows (e.g. 116 vascular plants in 0.9 ha) with high habitat diversity and soil pH were also characterised by high age (at least 115 years). Generally, accumulation of species with age in meadows towards species richness takes decades to centuries (Gibson & Brown 1992, Zobel 1992, van der Woude *et al.* 1994), but the effect may also be indirect via the development of specific soil characteristics, e.g. low nutrients (Eriksson *et al.* 1995). One such factor may be the C:N ratios increasing with age of meadow observed in our data, reducing soil N availability for plant uptake (Mengel & Kirby 1978, Killham 1994). For young traditional meadows (30–40 years old, for older meadows we lack information), we know that large amounts of dung were used at the time they were created in order to prevent weeds, thus the flora of these tends to indicate higher productivity than the flora of old traditional meadows. The correlation seen between age and species that are rare in our data may be due to the regionally rare species generally indicating nutrient-poor conditions, thus they cannot establish themselves before soil properties have developed from productive to nutrient-poor, which takes time (45 years for N-mineralization to decline was shown by Olff & Pegtel 1994). Another hypothesis is that dispersal capacity of small populations may be smaller due to lower output of dispersal agencies. Hence, species rarity may be caused by smaller dispersal ability and/or a smaller ability to establish at a site.

The species-rich meadows had a strong tendency to contain species that are rare, and regionally rare species are expected to occur among these. One mechanism whereby high species richness is correlated to the occurrences of species that are rare in our data may be that the most species-rich meadows have high habitat diversity, and many of these habitats are rare in our data-set and thus tend to contain rare species. In this way, the most species-rich meadows also contribute most to species richness in the region. Thus, local species richness and regional diversity are related as a result of nested habitats (Honnay *et al*. 1999; Å. Myklestad & M. Sætersdal unpubl. data).

Species richness of meadows was also strongly correlated to the number of species with narrow ecological tolerances. Low productivity, different habitats and higher soil pH in a meadow with time, probably enables a number of species with narrow tolerances according to Ellenberg *et al*. (1991) (habitat specialists) to establish, resulting in high species richness of the meadow. Vulnerable species are more likely to occur among species that are regionally rare and have narrow tolerances, suggesting that species richness and vulnerability are not independent in our data (Austrheim *et al*. 1999). Many vulnerable species may be habitat specialists, which, if the habitats are rare, again may explain why they are regionally rare (Rabinowitz *et al*. 1986). Extinctions are more likely to occur more rapidly if species are restricted to vulnerable habitats and have low local populations (Saunders *et al*. 1991, Austrheim *et al*. 1999). Thus, species-rich meadows are in great need of conservation. Our results suggest that many factors have to be present at the same time if a meadow is to be species-rich and contain regionally rare species, which is why these meadows are rare. Unproductive soil conditions are of primary importance, but do not by themselves guarantee high species numbers. Additionally, habitat diversity, high soil pH and high age will increase the species richness of meadows. This suggests that their recreation is difficult (e.g. Hughes & Huntley 1988, Dzwonko & Loster 1998), emphasizing the need for conservation of existing species-rich meadows.

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Appendix. Species list showing the frequency of each species within each management type (number of sites with species present divided by total site number within each management type).

	Traditional meadows *N* = 21	Lightly fertilized meadows *N* = 30	Artificially fertilized meadows *N* = 22	Intensively cultivated grasslands *N* = 28	Reforested meadows *N* = 29
Achillea millefolium	1.00	0.97	1.00	0.68	0.72
Achillea ptarmica	0.10	0.30	0.32	0.11	0.03
Acinos arvensis	0.19				0.07
Aconitum septentrionale	0.43	0.27	0.05		0.59
Actaea spicata					0.03
Aegopodium podagraria		0.03			
Agrostis canina		0.03			0.10
Agrostis capillaris	0.90	0.90	1.00	0.14	0.90
Agrostis stolonifera					0.03
Ajuga pyramidalis	0.38	0.30	0.41		0.14
Alchemilla alpina	0.57	0.43	0.23		0.38
Alchemilla spp.	0.86	0.90	1.00	0.61	0.66
Allium oleraceum		0.03	0.05		
Alnus incana	0.33	0.13	0.36		0.97
Alopecurus geniculatus			0.05	0.29	
Alopecurus pratensis	0.48	0.63	0.64	0.43	0.07
Anemone nemorosa	0.05				0.10
Anethum graveolens				0.04	
Angelica sylvestris	0.43	0.67	0.73	0.11	0.62
Antennaria dioica	0.48	0.13	0.09		0.17
Anthoxanthum odoratum	1.00	1.00	1.00	0.07	0.66
Anthriscus sylvestris	0.48	0.73	0.77	0.61	0.31
Anthyllis vulneraria	0.19	0.10	0.05		0.03
Aquilegia vulgaris	0.05		0.05		0.03
Arabis hirsuta	0.10				
Arabis petrea	0.05				0.03
Arabidopsis thaliana	0.10	0.10	0.09	0.04	
Arctium minus		0.07			0.07
Arctostaphylos uva-ursi	0.05				
Arenaria serpyllifolia			0.05	0.04	0.03
Arrhenatherum elatius		0.03	0.05	0.04	
Artemisia vulgaris	0.05			0.04	
Asplenium septentrionale	0.05				0.03
Asplenium trichomanes	0.05				0.14
Athyrium filix-femina	0.19	0.23	0.36		0.93
Atriplex spp.			0.05	0.32	
Avenula pratensis		0.03			
Avenula pubescens	0.05	0.03	0.09		
Barbarea vulgaris	0.05			0.04	
Bartsia alpina	0.05				
Berberis vulgaris					0.07
Betula pendula		0.13	0.09		0.34
Betula pubescens	0.33	0.07	0.09		0.72
Bistorta vivipara	0.76	0.47	0.36	0.04	0.24
Botrychium lunaria	0.29	0.03			
Brachytecium pinnatum				0.04	
Brassica oleraceum				0.11	
Briza media	0.14	0.10			0.03
Bromus inermis				0.11	
Bromus tectorum	0.14	0.13	0.05		
Calamagrostis epigeios					0.17

Continues

Appendix. Continued.

	Traditional meadows $N = 21$	Lightly fertilized meadows $N = 30$	Artificially fertilized meadows $N = 22$	Intensively cultivated grasslands $N = 28$	Reforested meadows $N = 29$
Calamagrostis purpurea	0.05		0.09		0.17
Calluna vulgaris	0.38	0.03	0.05		0.17
Caltha palustris	0.29	0.17	0.05	0.04	0.07
Campanula cervicaria	0.05	0.03			
Campanula glomerata		0.03			
Campanula latifolia					0.03
Campanula rotundifolia	1.00	0.83	0.77	0.07	0.93
Capsella bursa-pastoris		0.03		0.68	
Carduus crispus			0.05	0.07	
Cardamine flexuosa		0.10	0.09	0.04	0.14
Cardamine pratensis	0.05	0.17	0.18	0.07	
Carex canescens	0.05	0.03	0.05		
Carex capillaris	0.05				0.03
Carex demissa	0.14	0.03			0.07
Carex echinata	0.05				0.14
Carex flava	0.10				0.07
Carex muralis					0.03
Carex nigra	0.38	0.27	0.18	0.04	0.03
Carex ovalis	0.29	0.47	0.32		0.03
Carex pallescens	0.76	0.77	0.41		0.79
Carex panicea	0.48	0.23	0.09		0.14
Carex pilulifera	0.57	0.50	0.14		0.17
Carex pulicaris		0.03			
Carex rupestris					0.03
Carex serotina	0.10		0.05		
Carex vaginata	0.05				
Carum carvi	0.62	0.60	0.50		0.10
Centaurea jacea	0.24	0.30	0.09		0.10
Cerastium alpinum	0.05				0.07
Cerastium fontanum	0.71	0.63	0.59	0.46	0.62
Chamomilla suaveolens		0.03	0.05	0.36	
Chrysosplenium alternifolium		0.03			
Cicerbita alpina		0.03			
Circaea alpina					0.45
Circaea intermedia					0.07
Cirsium arvense		0.03			
Cirsium helenoides	0.52	0.60	0.50	0.07	0.66
Cirsium palustre	0.19	0.10	0.05		0.34
Cirsium vulgare			0.05	0.04	0.10
Clinopodium vulgare	0.14	0.03	0.05		0.28
Coeloglossum viride	0.05				
Conopodium majus	0.05				
Convallaria majalis					0.07
Corylus avellana	0.05		0.09		0.45
Cotoneaster scandinavicus	0.10				0.10
Crepis paludosa	0.19	0.03	0.05		0.28
Crepis tectorum	0.10				
Cryptogramma crispa	0.05				
Cynosurus cristatus	0.10	0.03			
Cystopteris fragilis	0.05		0.05		0.38
Dactylorhiza fuchsii	0.19	0.03	0.05		0.10
Dactylorhiza maculata	0.05	0.07	0.09		0.07

Continues

Appendix. Continued.

	Traditional meadows $N = 21$	Lightly fertilized meadows $N = 30$	Artificially fertilized meadows $N = 22$	Intensively cultivated grasslands $N = 28$	Reforested meadows $N = 29$
Dactylis glomerata	0.81	0.77	0.95	0.71	0.69
Dantonia decumbens	0.29	0.20	0.09	0.04	0.03
Daucus carota		0.03		0.07	0.03
Deschampsia cespitosa	0.81	0.97	1.00	0.39	1.00
Deschampsia flexuosa	0.86	0.63	0.68	0.04	0.83
Dianthus deltoides	0.10	0.07			
Digitalis purpurea	0.05	0.03			0.07
Draba incana	0.10				
Dryopteris filix-mas	0.14	0.13			0.62
Elymus canina					0.55
Elymus repens	0.05		0.05	0.39	
Empetrum nigrum	0.10				0.03
Epilobium angustifolium	0.10	0.03	0.14		0.21
Epilobium collinum	0.10	0.03	0.05		0.07
Epilobium hornemannii		0.03			0.03
Epilobium montanum		0.07	0.09		0.72
Equisetum arvense	0.43	0.23	0.41	0.07	0.24
Equisetum pratense	0.10	0.27	0.18	0.07	0.03
Equisetum sylvaticum	0.05		0.05		0.10
Erigeron borealis	0.14				
Eriophorum latifolium	0.05				0.03
Erodium cicerbitum	0.05				
Erophila verna	0.10	0.03			
Euphrasia spp.	0.43	0.23	0.23	0.04	0.03
Festuca ovina	0.38	0.23	0.18		0.17
Festuca pratensis	0.43	0.30	0.36	0.64	0.07
Festuca rubra	0.90	0.83	0.73		0.45
Festuca vivipara	0.10				
Filaginella uliginosa				0.04	
Filipendula ulmaria	0.52	0.77	0.64	0.25	0.83
Fragaria vesca	0.76	0.60	0.50		0.93
Frangula alnus	0.05		0.05		0.07
Fraxinus excelsior	0.14	0.10	0.14		0.31
Fumaria officinalis				0.04	
Gagea lutea		0.07			
Galeopsis bifida	0.05	0.03		0.07	0.79
Galeopsis speciosa	0.14	0.17	0.18	0.04	0.07
Galeopsis tetrahit		0.03		0.04	0.31
Galium album	0.29	0.27	0.45	0.18	0.07
Galium aparine		0.03		0.07	0.07
Galium boreale	0.86	0.87	0.86		0.83
Galium odoratum					0.07
Galium palustre	0.05				0.14
Galium saxatile	0.10	0.03	0.09		
Galium triflorum		0.07			
Galium uliginosum	0.62	0.40	0.27		0.41
Galium verum	0.38	0.50	0.50		0.14
Gentianella campestris	0.19				
Geranium robertianum	0.05	0.03			0.45
Geranium sylvaticum	0.90	0.90	0.77	0.14	0.83
Geum rivale	0.57	0.63	0.50	0.04	0.69
Geum urbanum	0.05	0.07			0.69

Continues

Appendix. Continued.

	Traditional meadows *N* = 21	Lightly fertilized meadows *N* = 30	Artificially fertilized meadows *N* = 22	Intensively cultivated grasslands *N* = 28	Reforested meadows *N* = 29
Glechoma hederacea		0.03			
Glyceria fluitans				0.04	
Gymnadenia conopsea	0.52	0.20			
Gymnocarpium dryopteris	0.24	0.07	0.14		0.62
Heracleum sibiricum			0.05		
Heracleum sphondylium	0.10	0.20	0.23	0.07	0.03
Hieracium pilosella	0.95	0.70	0.59		0.21
Hieracium scandinavicum	0.05	0.07			
Hieracium suecicum			0.09		
Hieracium sylvaticum					0.55
Hieracium umbellatum	0.43	0.50	0.50		0.38
Hieracium vulgata	0.38	0.27	0.18		0.03
Holcus lanatus		0.20	0.27		
Holcus mollis		0.03			0.14
Humulus lupulus		0.03			
Huperzia selago					0.03
Hypericum maculatum	0.86	0.90	0.86		0.93
Hypericum perforatum	0.14				0.17
Hypochoeris maculata	0.10	0.20	0.14		
Hypochoeris radicata		0.03			
Impatiens noli-tangere					0.34
Impatiens parviflora					0.03
Juncus articulatus	0.10		0.05		0.10
Juncus bufonius		0.03		0.04	
Juncus effusus	0.05				
Juncus filiformis	0.14	0.23	0.14		0.03
Juniperus communis	0.33	0.07	0.14		0.66
Knautia arvensis	0.86	0.93	0.77		0.59
Lamium purpureum				0.11	
Lappula deflexa					0.07
Lapsana communis					0.03
Lathyrus linifolius	0.19	0.07	0.14		0.10
Lathyrus pratensis	0.38	0.20	0.14		0.10
Leontodon autumnalis	0.24	0.37	0.45	0.32	
Leucanthemum vulgare	0.81	0.83	0.77	0.21	0.31
Linaria vulgaris	0.24	0.13	0.27	0.04	0.21
Linnaea borealis					0.10
Linum cartharticum	0.24	0.07			0.07
Listera ovata	0.10				
Lolium multiflorum				0.04	
Lolium perenne			0.05	0.43	
Lotus corniculatus	0.90	0.63	0.73	0.04	0.24
Luzula multiflora	0.90	0.97	0.95		0.52
Luzula pilosa	0.14	0.10	0.14		0.28
Luzula spicata	0.10				
Luzula sylvatica	0.05				0.03
Lychnis viscaria	0.24	0.53	0.41	0.04	0.03
Maianthemum bifolium	0.10	0.03	0.05		0.17
Matricaria maritima		0.03		0.04	
Matricaria perforata			0.05	0.39	
Matteuccia struthiopteris	0.05				0.03
Melampyrum pratense	0.33	0.07	0.23		0.34

Continues

Appendix. Continued.

	Traditional meadows *N* = 21	Lightly fertilized meadows *N* = 30	Artificially fertilized meadows *N* = 22	Intensively cultivated grasslands *N* = 28	Reforested meadows *N* = 29
Melampyrum sylvaticum	0.10	0.03			0.24
Melica nutans	0.14	0.03			0.55
Mentha arvensis	0.05				
Milium effusum					0.07
Minuartia bifolia					0.03
Moehringia trinervia					0.10
Molinia caerulea	0.43	0.10			0.34
Mycelis muralis					0.14
Myosotis arvensis	0.62	0.50	0.45	0.14	0.34
Myosotis laxa		0.03			0.03
Myosotis scorpioides	0.05	0.07	0.14		
Myosotis stricta		0.03	0.05		
Nardus stricta	0.48	0.30	0.05		0.07
Omalotheca norvegica	0.10	0.10			
Omalotheca sylvatica		0.07	0.14		0.03
Orchis mascula	0.05	0.10			0.03
Origanum vulgare	0.24	0.07			0.28
Orthilia secunda					0.03
Oxalis acetosella	0.10	0.07	0.09		0.90
Oxyria digyna					0.03
Paris quadrifolia					0.24
Parnassia palustris	0.05				0.03
Persicaria maculoca				0.07	
Phalaris arundinaceae	0.05		0.05	0.07	0.10
Phegopteris connectilis	0.19	0.07	0.09		0.76
Phleum alpinum	0.10	0.20	0.05		
Phleum pratense	0.38	0.53	0.59	0.82	0.03
Picea abies					0.34
Pimpinella saxifraga	0.57	0.63	0.45		0.38
Pinguicula vulgaris	0.14				0.03
Pinus sylvestris	0.14				0.24
Plantago lanceolata	0.67	0.63	0.68		0.24
Plantago major	0.10	0.13	0.32	0.14	0.07
Plantago media	0.05		0.05		
Platanthera bifolia	0.19	0.03			
Platanthera chlorantha	0.05	0.03	0.05		
Poa alpina	0.10				
Poa annua	0.14	0.23	0.36	0.68	0.21
Poa flexuosa	0.05				
Poa glauca	0.29	0.13			0.28
Poa nemoralis	0.14	0.10			0.79
Poa pratensis	0.86	0.83	0.91	0.36	0.34
Poa trivialis	0.29	0.27	0.23	0.79	0.41
Polypodium vulgare	0.05		0.05		0.45
Polygonum aviculare		0.03	0.05	0.43	
Polystichum lonchitis					0.10
Polygonatum odoratum					0.07
Polygonatum verticillatum	0.05				0.17
Populus tremula	0.33	0.27	0.27		0.55
Potentilla argentea	0.57	0.47	0.36	0.14	0.28
Potentilla crantzii	0.43	0.10			
Potentilla erecta	0.86	0.80	0.77		0.93

Continues

Appendix. Continued.

	Traditional meadows *N* = 21	Lightly fertilized meadows *N* = 30	Artificially fertilized meadows *N* = 22	Intensively cultivated grasslands *N* = 28	Reforested meadows *N* = 29
Potentilla palustris					0.03
Polygala vulgaris	0.24	0.07	0.05		
Prunus avium		0.03			
Prunus padus		0.13	0.14	0.04	0.83
Prunella vulgaris	0.67	0.57	0.41		0.41
Pteridium aquilinum	0.19	0.17	0.05		0.55
Pyrola minor	0.05				
Quercus spp.					0.03
Ranunculus acris	0.95	0.97	1.00	0.39	0.93
Ranunculus auricomus	0.05	0.13	0.23	0.04	
Ranunculus ficaria			0.05		
Ranunculus repens	0.33	0.33	0.45	0.93	0.66
Rhinanthus minor	0.86	0.67	0.68	0.04	0.10
Rhodiola rosea					0.03
Ribes rubrum			0.05		0.07
Ribes uva-ursi					0.07
Rorippa palustris				0.11	
Rorippa sylvestris		0.03			
Rosa canina	0.05	0.03			
Rosa dumalis	0.05	0.03	0.09		
Rosa majalis	0.05				
Rubus idaeus	0.48	0.57	0.68	0.04	1.00
Rubus saxatilis	0.57	0.13	0.32	0.04	0.69
Rumex acetosa	1.00	0.93	0.91	0.79	0.93
Rumex acetosella	0.67	0.53	0.50	0.07	0.45
Rumex crispus		0.03	0.14	0.07	
Rumex longifolius	0.10	0.13	0.18	0.86	
Sagina nodosa					0.10
Sagina procumbens	0.14				0.03
Sagina saginoides	0.05				
Salix caprea	0.24	0.13	0.18		0.34
Salix lapponum	0.05				
Salix myrtilloides					0.03
Salix phyllicifolia	0.05				
Sambucus spp.					0.03
Saussurea alpina	0.10				0.10
Saxifraga adscendens	0.05				
Saxifraga aizoides	0.10				0.07
Saxifraga nivalis					0.07
Scleranthus annuus	0.10	0.10	0.05		0.03
Scleranthus perennis	0.05	0.03			0.03
Scrophularia nodosa					0.03
Sedum acre	0.38	0.23	0.14		0.24
Sedum album	0.14	0.07	0.05		0.14
Sedum annuum	0.52	0.33	0.27		0.10
Sedum villosum	0.10				
Senecio jacobea					0.03
Senecio sylvaticus				0.04	
Silene acaulis	0.05				
Silene dioica	0.33	0.43	0.27	0.21	0.62
Silene latifolia		0.07		0.04	

Continues

Appendix. Continued.

	Traditional meadows *N* = 21	Lightly fertilized meadows *N* = 30	Artificially fertilized meadows *N* = 22	Intensively cultivated grasslands *N* = 28	Reforested meadows *N* = 29
Silene rupestris	0.62	0.43	0.23		0.38
Silene vulgaris	0.67	0.67	0.59	0.04	0.59
Solidago virgaurea	0.29	0.17	0.18		0.66
Sorbus aucuparia	0.43	0.40	0.32		0.93
Sorbus hybrida					0.03
Spergula arvensis		0.03		0.14	
Stachys palustris		0.03			
Stachys sylvatica	0.05				0.48
Stellaria alsine		0.03			
Stellaria graminea	0.57	0.50	0.59	0.21	0.48
Stellaria media	0.10	0.07	0.27	0.64	0.07
Stellaria nemorum	0.14	0.03			0.41
Succisa pratensis	0.05	0.03	0.05		0.31
Tanacetum vulgare	0.05				
Taraxacum sect. *Ruderalia*	0.62	0.63	0.91	0.89	0.45
Thlaspi caerulescens	0.24	0.23	0.41	0.14	0.07
Tilia cordata					0.03
Trientalis europea	0.10	0.20	0.05		0.52
Trifolium dubium		0.07			
Trifolium hybridum				0.14	
Trifolium medium	0.24	0.40	0.18	0.04	0.28
Trifolium pratense	1.00	0.90	1.00	0.89	
Trifolium repens	0.90	0.83	0.95	0.86	0.24
Triglochin palustris	0.05				
Tussilago farfara					0.14
Ulmus glabra					0.21
Urtica dioica	0.52	0.47	0.64	0.71	0.72
Vaccinium vitis-idaea	0.19	0.03	0.05		0.28
Vaccinium myrtillus	0.52	0.33	0.32		0.66
Vaccinium uliginosum	0.19				
Valeriana sambucifolia	0.19	0.23	0.36		0.76
Verbascum nigrum	0.05	0.03	0.09		0.03
Verbascum thapsus		0.03			
Veronica arvensis	0.29	0.20	0.23		
Veronica chamaedrys	0.76	0.70	0.77		0.59
Veronica fruticans	0.05				
Veronica officinalis	0.81	0.70	0.64		0.83
Veronica persicaria			0.09		
Veronica serpyllifolia	0.29	0.40	0.45	0.14	0.10
Veronica verticillata		0.03			
Viburnum opulus					0.17
Vicia cracca	0.76	0.70	0.64	0.32	0.38
Vicia sepium	0.29	0.47	0.36	0.14	0.45
Vicia sylvatica	0.05				0.10
Viola biflora					0.03
Viola canina	0.71	0.60	0.45		0.48
Viola mirabilis					0.21
Viola palustris	0.43	0.27	0.32		0.62
Viola riviniana	0.14	0.07	0.23		0.83
Viola tricolor	0.71	0.73	0.59	0.29	0.21
Woodsia ilvensis	0.29	0.07	0.05		0.31