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Research article

A comparison of plant communities on the basis of their clonal growth patterns

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Abstract. This study was performed to analyse how a vegetative propagation pattern of plants affects the coexistence of species and subsequent species richness of the community. We compared community average clonal growth in the herbal communities of forests, wooded meadows, and open meadows in Laelatu, Estonia. The parameters used for the calculation of the community averages and measured for each species were ramet life span, rhizome branching, and clonal mobility. We also examined the intrinsic (i.e. independent of the environment) relationship between community clonal growth and plant species density. We found strong correlations between the environmental factors (productivity, light availability, and mowing regime) and community averages of clonal growth parameters, while species density was (negatively) correlated only with community average of rhizome increment. The community average of ramet life span decreased with the increasing biomass of the herb layer. No evidence was found to support the hypothesis that species-rich communities may consist of species with more contrasting mobility compared with species-poor communities. Independent of the effect of the environmental factors, species density was positively correlated with ramet density. There was intrinsic positive relationship between species density and community average of ramet life span at open meadow sites and intrinsic negative relationship between species density and community average of rhizome increment at wooded meadow sites. We conclude that in forest communities the capability of clonal plants to forage for light is favoured, while in unmown meadows a competitively strong phalanx growth form is advantageous. We established that ramet turnover increases and vegetative mobility decreases with increasing species diversity, although these two relationships depend strongly on the type of the studied community.

Key words: clonal growth, ramet life span, ramet turnover, species diversity, vegetative mobility, vegetative propagation

Introduction

The nature of the relationship between the patterns of vegetative propagation and the species richness of a plant community has not yet been generally established. There are records of several extremely species-rich plant communities which consist mainly of clonal plants (Kull and Zobel, 1991; Kukk and Kull, 1997; Klimeš, 1999). However, it is not known to what extent species richness is associated with the properties of clonal spreading, or with the mode of the reproduction of constituent species in a particular community. Some attempts have been made to estimate the role of species turnover in species coexistence (e.g. Rusch and van der Maarel, 1992; van der Maarel and Sykes, 1993; Herben *et al.*, 1993,1994; Klimeš, 1999), whereas small-scale species turnover itself evidently depends on some features of clonal growth, e.g. ramet life span and vegetative mobility. Yet the existence of a relationship between species richness and the clonal growth characteristics of the constituent species in a community has remained basically unexplored (but see Herben *et al.*, 1997; Klimeš, 1999; Song *et al.*, 2002; Sammul *et al.*, 2003).

Numerous studies have described variation of the clonal growth characteristics of species or individual clones along environmental gradients (see Hutchings and de Kroon, 1994; de Kroon and Hutchings,1995 for a review) and the arising foraging behaviour (Sutherland and Stillman, 1988; Cain, 1994; Oborny, 1994; Piqueras *et al.*, 1999). It has been shown that the ability to vary clonal growth in response to a changing environment is species-specific, while there also are species that almost lack this ability (de Kroon and Hutchings, 1995). Moreover, there are only a few species whose plasticity of growth is sufficiently large to adequately respond to environmental heterogeneity occurring in the nature (Hutchings and de Kroon, 1994; Stuefer, 1996).

Similar studies on the community level, i.e. studies where communities were compared on the basis of the clonal growth of all species to some other community (e.g. Pokarzhevskaya, 1995; Tamm *et al.*, 2002; Song *et al.*, 2002) or to the same community after some kind of perturbation (e.g. fertilisation in Sammul *et al.*, 2003), are very scarce. Mostly, some permanent plot has been mapped with high spatial resolution and the spatio-temporal dynamics of the shoots in this plot has been observed (e.g. Rusch and van der Maarel, 1992; van der Maarel and Sykes, 1993; Herben *et al.*, 1994; Pärtel and Zobel, 1995). These studies have demonstrated that there exists considerable turnover of species on both the spatial and the temporal scales, and that such turnover differs among species (Thórhallsdóttir, 1990; Rusch and van der Maarel, 1992; van der Maarel and Sykes, 1993; Herben *et al.*, 1994; Law *et al.*, 1994; Sykes *et al.*, 1994) as well as among communities (Herben *et al.*, 1994; Pärtel and Zobel, 1995). It has been shown that disturbance, such as drought, may enhance shoot mobility (van der Maarel, 1996) and that higher shoot mobility can be found in communities with higher species richness (Sykes *et al.*, 1994). On the other hand, Pärtel and Zobel (1995) found that during successional changes the speed of shoot mobility did not change. Herben *et al.* (1994) found fairly similar shoot mobility in communities with different species richness and Klimeš (1999) showed that low shoot mobility does not contradict high species richness.

The findings concerning the relationship between shoot mobility and species richness are highly variable partly also because of methodological peculiarities. Analysis of only the data of shoots locations does not allow to discriminate between different types of reproduction and mobility. It appears necessary to distinguish between shoot mobility or shoot turnover, as detected from shoot data, and vegetative mobility or clonal mobility which describes the ability of a clone to move in space using its vegetative organs (rhizomes, stolons, etc.) and to alter the location of its ramets (Tamm *et al.*, 2002). Analysis of shoot turnover in permanent plots is not well applicable in species-poor systems, where most shoots belong to a few species and the real extent of shoot turnover and mobility of ramets remains therefore undetected. Also, this method is rather time-consuming.

Another approach for comparison of community-level differences in clonal growth (Tamm *et al.*, 2002; Sammul *et al.*, 2003; see also Kull, 1995a) assumes that the characteristics of clonal growth are species-specific and do not substantially change with changing environmental conditions (see Stuefer, 1996 for discussion of relevant variability of clonal growth). The community-level estimates of clonal growth can then be obtained by calculating the weighted average of a clonal growth parameter using some estimate of the abundance of each constituent species in the community as a weight (e.g. Sammul *et al.*, 2003).

Average clonal growth in the community may change with changing environmental conditions in several ways. For example, species with a particular type of clonal growth may prevail in certain conditions; e.g. increased level of vegetative mobility due to higher abundance of rhizomatous legumes in the community (Sammul *et al.*, 2003), reduced share of vegetatively mobile species in high alpine communities, where long runners can be damaged by the moving soil during cold winter (Pokarzhevskaya, 1995), or increased abundance of phalanx plants in communities with lower availability of soil nitrogen and lesser precipitation (Song *et al.*, 2002). On the other hand, some communities may consist of species with similar clonal growth, whereas some other communities may consist of species with fairly different clonal growth and leading thus to increase in variation of clonal growth among the coexisting species. It has been shown that interspecific differences in mobility promote coexistence in modeled communities (Bell, 1984; Caswell and Cohen, 1991) as well as in experimental communities (Schmid and Harper, 1985). If the inferior competitor is more mobile than the superior one, it may avoid competitive exclusion by moving to a more favourable spot (Klimeš, 1999).

Both species richness and community average of clonal growth depend directly on the composition of the vegetation. Thus, in statistical sense they are not independent and should not be compared directly except for estimation of correlation. However, while species richness is a mere measure of the size of a species list, community average of clonal growth also accounts for the structure of the vegetation. Whether a clonal growth pattern exerts a direct effect on the species richness of the community can be best tested by setting up an appropriate experiment. However, estimation of the partial correlation coefficients or application of path analysis would also provide an insight into the intrinsic relationship between species richness and clonal growth. At present, we are not aware of any study where the simultaneous effect of the environment on species richness and on community clonal growth were excluded prior to estimation of the relationship between the two. Thus it is not known to what extent changes in the mobility pattern of ramets in a community directly affect the species diversity of the community, or to what extent they merely co-vary due to variation in environmental conditions.

In this study we aimed at estimating the relationship between community clonal growth and a few important community characteristics (aboveground biomass of the herb layer, availability of light to the herb layer, mowing frequency, species density, and ramet density) in three different types of communities: deciduous forest, wooded meadow and open meadow. We compared the clonal growth pattern of the three community types. Also, we specifically focused on the relationships found, or hypothesised in earlier studies:

(1) Is high clonal mobility of species characteristic to communities with high species richness?
(2) Is species richness correlated with ramet turnover, or the proportion of species with a long life span of ramets in the community?
(3) Do species-rich communities consist of species with more contrasting mobility compared with species-poor communities?

We assumed in our analysis that all community-wide clonal growth parameters are dependent on and co-vary with species composition. Hence we first estimated the influence of the main environmental variables (mowing, community productivity, light availability) on the parameters associated with the changing vegetation. Further, we estimated the intrinsic relationships between average clonal growth in the community, ramet density, and species density, which are not caused by co-variation with the environmental variables.

Methods

Study area

Laelatu wooded meadow is located on the western coast of Estonia (lat. 58°35′15″ N, long. 23°33′00″ E) on the West Estonian Lowland. It forms part of the Laelatu-Puhtu-Nehatu Nature Reserve. The total area of the meadow is 150 ha, but today only ca 15 ha are mown regularly (Kukk and Kull, 1997). The area has been exploited for at least 300 years for hay cutting. There are no reports to that this area has ever been grazed by domestic animals. The area emerged from the sea 1000–2000 years ago (Sepp and Rooma, 1970) and belongs to the boreo-nemoral zone. The soil is rendzic leptosol with a pH of 6.7–7.2 and lies on Silurian limestone bedrock covered with calcareous moraine. The humus layer is thin (15–20 cm) and relatively poor in available nutrients (Sepp and Rooma, 1970). Mean temperature for July is 17 °C and for January −5 °C. Annual mean temperature is 6.3 °C in the air and 7.1 °C on the ground. Mean annual precipitation is 500–600 mm, the most rainy seasons are late summer and autumn.

The vegetation of Laelatu wooded meadow is characterised by a very high species richness and species density. The maximum number of vascular plant species in a 20 × 20 cm plot is 42 and in a 1 × 1 m plot 76 (Kull and Zobel, 1991; Kukk and Kull, 1997; Kukk pers. comm.). The flora of vascular plants in Laelatu wooded meadow and in adjacent areas comprises 470 species, while 225 species are known directly from the wooded meadow (Kukk and Kull, 1997). The bryoflora of Laelatu consists of 96 species (Ingerpuu *et al.*, 1998). The vegetation belongs mostly to the *Sesleria coerulea – Filipendula hexapetala* association (Krall and Pork, 1970). The tree layer (crown projections) covers on average 30–50% of the ground surface and consists of *Quercus robur* L., *Betula spp*. L., *Fraxinus excelsior* L., *Populus tremula* L., etc. (Kukk and Kull, 1997; nomenclature after Kukk, 1999). The abandoned parts of the wooded meadow are nowadays covered with deciduous forests of different age. The dominant tree species in the forests are *Betula spp.*, *Fraxinus excelsior*, *Populus tremula* and *Alnus incana* (L) Moench.

The study area provides a wide range of environmental gradients in a relatively limited area. The soil layer of the land that lifted from the sea earlier is shallower and dryer. In case these spots are not overgrown with forest, they have lower productivity and often also higher species density. The lower parts of the meadow are moister, have higher productivity and lower species density. The variable tree cover absorbs different amounts of light and provides different levels of irradiance for the ground layer. The gradients of available light, soil moisture and productivity are related to each other. Combined with the history of the management (mowing) of the area, they determine local species density. Spots with continuous mowing (once a year) for at least over 40 years, moderate moisture conditions, low (but not the lowest) productivity and less than 50% tree cover are the most species rich (over 60 species of vascular plants per square metre).

Vegetation census

A total of 104 vegetation analyses were carried out using 1 m^2 plots. The plots were located at 13 different sites: 5 sites of deciduous forest and overgrown wooded meadow, 4 sites of wooded meadow with a medium tree cover, and 4 sites of open or treeless calcareous meadow. The communities were chosen to

Table 1. General characteristics of studied sites. Aver. stands for average and St.Err. stands for respective standard error

Site	No. of relevés	Mowing frequency (times/year)	Living biomass of ground layer (g/m^2)		Light penetration coefficient (%)		Species density (no./m^2)		Ramet density (no. × 10^3/m^2)	
			Aver.	St. Err.	Aver.	St. Err.	Aver.	St. Err.	Aver.	St. Err.
Open site 1	8	0.2	664	129	54	3.44	20	2.25	1.6	0.28
Open site 2	8	0.1	463	55	91	0.65	16	1.93	5.7	0.76
Open site 3	11	0.2	443	61	84	0.75	22	1.67	6.3	0.47
Open site 4	8	1.0	262	17	54	5.71	43	2.77	3.2	0.24
Wooded meadow 1	8	0.5	172	25	14	1.95	35	2.83	1.8	0.20
Wooded meadow 2	8	0.6	318	21	27	5.61	30	2.96	2.4	0.23
Wooded meadow 3	8	0.7	327	27	29	6.38	34	1.73	2.6	0.25
Wooded meadow 4	8	1.0	301	57	37	7.20	48	1.75	3.5	0.40
Forest site 1	8	0	99	22	3	0.66	9	0.75	0.71	0.19
Forest site 2	8	0	128	24	5	0.44	14	1.06	0.65	0.61
Forest site 3	7	0	168	22	5	1.90	13	0.59	0.59	0.89
Forest site 4	6	0	167	29	3	0.80	13	1.52	0.67	0.14
Forest site 5	8	0	93	7	5	1.19	17	1.41	0.52	0.63
Average of open sites			457	43	72	3.21	25	1.99	4.4	0.40
Average of wooded meadows			279	20	27	3.08	37	1.68	2.6	0.17
Average of forests			128	10	4	0.48	13	0.65	0.63	0.05

provide the full gradient of direct sunlight available to the ground layer. The list of plant species indicates that mesic conditions prevail in all studied communities.

Mostly 8 plots per community were analysed (Table 1). In each plot, all species were recorded and their cover was estimated. In addition, the number of ramets (ramet is a shoot with a part of the stolon or rhizome connecting it with its parent shoot) was counted in two $0.1 \times 0.25\ \mathrm{m}^2$ subplots within each plot. The subplots were located in the opposite corners of the $1\ \mathrm{m}^2$ plot 10 cm from both of its nearest sides. All shoots in the subplot were cut close to the ground layer, collected, dried at 80 °C for 48 h and weighed with an accuracy of 0.1 g to estimate the phytomass of the community. For each community, the frequency of mowing was recorded using the information obtained from the managers of the area. Light availability to the ground layer was measured above the herb layer by using hemispherical 'fish-eye' photographs (Anderson 1964). A camera (model OM-2S, Olympus Optical Co., Ltd, Tokyo, Japan) with an 8 mm fish-eye lens was vertically aligned with the top of the camera facing north. For every plot, one photograph was taken just above the herb layer. From every photograph, the relative amount of canopy (trees and shrubs) gap was measured with respect to the zenith angle. Light penetration coefficient (L) was then calculated as the fractional transmission of diffuse irradiance on the horizontal plane:

$$L = \frac{\pi}{9} \sum_{\alpha=5^\circ,15^\circ\ldots}^{85^\circ} g_\alpha \sin\alpha \cos\alpha \tag{1}$$

Here g_α is the gap fraction within a 10° zenith angle interval ($\alpha - 5^\circ$, $\alpha + 5^\circ$). No correction for direct sunlight was made.

Data of the clonal characteristics of species

The clonal fragments (polycormons) of 120 most abundant species of Laelatu wooded meadow were excavated between 1988 and 1997 for the measurement of the clonal growth parameters. Most excavations took place in 1995–1996. For each species at least 10 clonal fragments were collected. The number of ramets collected in this way per species was in most cases between 50 and 100.

Based on the scars from the dead shoots on the rhizomes as well as the size and morphology of the internodes and nodes on the rhizomes, ramet age was estimated, the annual increment of their rhizome parts was measured, and the number of the rhizome branches per ramet was counted (Tamm *et al.*, 2002; Sammul *et al.,* 2003; detailed results of these measurements will be published elsewhere and are partly presented within the above references). If a ramet is annual, as is the case with most species of Laelatu (see appendices in Tamm *et al.*,

Table 2. Average values of community clonal growth parameters and respective standard errors (St. Err.)

Site	Ramet life span (yr)		Rhizome increment (mm/yr)		Branching intensity (ramets/ramet year)	
	Average	St. Err.	Average	St. Err.	Average	St. Err.
Open site 1	2.06	0.10	21.5	2.9	0.53	0.06
Open site 2	1.37	0.04	8.1	0.4	0.80	0.03
Open site 3	1.58	0.04	9.6	0.4	0.83	0.03
Open site 4	2.77	0.08	29.0	6.7	0.64	0.02
Wooded meadow 1	2.92	0.16	71.1	7.1	0.54	0.03
Wooded meadow 2	3.05	0.10	81.1	5.8	0.65	0.03
Wooded meadow 3	2.42	0.10	24.0	1.9	0.67	0.04
Wooded meadow 4	2.29	0.12	29.0	2.4	0.70	0.02
Forest site 1	2.67	0.52	54.7	20.2	0.62	0.12
Forest site 2	3.10	0.18	63.7	7.0	0.50	0.04
Forest site 3	2.72	0.23	69.5	9.2	0.41	0.06
Forest site 4	3.93	0.39	109.1	15.5	0.40	0.05
Forest site 5	2.96	0.23	87.6	6.1	0.39	0.04
Average of open meadow sites	1.91	0.10	16.4	2.2	0.71	0.03
Average of wooded meadow sites	2.67	0.08	51.3	5.1	0.64	0.02
Average of forest sites	3.04	0.16	75.4	6.2	0.47	0.03

2002 and Sammul *et al.*, 2003), each separate rhizome branch has been formed within one year. If a ramet is perennial, it mostly does not move horizontally after the first year (e.g. most of the *Carex* spp. in the flora of Laelatu, see Tamm *et al.*, 2002 for description). Owing to strong seasonality at the latitude of the studied communities, most species have differences in the formation of nodes and internodes in different seasons. In spring the internodes of the rhizome are commonly longer and thinner than the internodes that will grow later in the year (e.g. in *Sesleria coerulea*), which leads to a characteristic structure of the thinner and thicker parts of the rhizome representing the yearly growth of the rhizome. Very often there is clear segmentation of the rhizome in species with perennial ramets (e.g. *Primula veris*, *Filipendula vulgaris*) due to cessation of growth in winter. In this case one segment is the product of the yearly growth of the rhizome. Usually, also the part of the rhizome that has grown during the current year differs in colour from the older parts of freshly excavated rhizomes. Frequently, remains of old leaves on the rhizome denote the place where the shoot was growing. Such morphological differences allow to estimate ramet age and yearly growth of the rhizome (see also Tamm *et al.,* 2002; Sammul *et al.,* 2003).

For all other means of vegetative reproduction, besides rhizomes (bulbils, stolons, shoots from root buds), the same characteristics were measured. The distance between the shoot of the previous year and the one of the current year can be estimated from the remains of old bulbils. No species with bulbils had perennial ramets in our samples. The only species with regular resprouting from roots was *Ophioglossum vulgatum*, for which the length of the root part from the "mother" ramet to the "daughter" shoots sprouting from root buds was measured and treated as a measure of vegetative mobility. The age of a ramet of *O. vulgatum* can be estimated by counting the rhizome segments as it forms one segment per year.

Measurement of clonal fragments has been long practised in studies of clonal growth (e.g. Harper and White, 1974; Pitelka *et al.,* 1985; Callaghan, 1988). Although the most accurate estimate of yearly growth of ramets can be obtained by following the ramets over time, this procedure is not suitable for measuring large numbers of species in their natural conditions. As weather conditions change from year to year, the results obtained by following the growth of ramets in time would be only current-year specific, while measurement of the rhizomes retrospectively accounts for the yearly differences. Moreover, it is usually impossible to establish the parent–daughter relationships in order to correctly estimate the intensity of vegetative propagation by observing only the above-ground parts (Pitelka *et al.*, 1985). It would also be an extremely long-term project to estimate ramet life span using observational data. The retrospective approach used in this study obviates the need for prolonged observations (Callaghan *et al.*, 1989) and enables to estimate all three main characteristics of vegetative propagation (number of offspring, distance between ramets from different generations, and ramet age) at the same time. There are a few species with perennial and potentially very old (several decades) ramets in the case of which estimation of ramet age from rhizomes is not possible as their older parts decay (e.g. *Pinguicula vulgaris*, *Succisa pratensis*). However, as such ramets may live even several decades (Ehrlén and Lehtilä, 2002), their age can not be estimated easily from observations either. It has been shown that measurement of plant rhizomes often yields highly accurate estimation of the life history of the clone (e.g. Pitelka *et al.*, 1985; Callaghan *et al.,* 1986; Kull, 1995b).

From the measurement of the clonal fragments, the following parameters were calculated for each species: median of ramet life span, median of branching intensity (number of rhizome branches per ramet per year), and median of rhizome increment per year. The median was chosen instead of the average owing to the highly asymmetric distribution of these variables within species. As it was impossible to transform the variables to fit normal distribution, distribution-independent parameters had to be employed.

For several species, found in vegetation analyses with low frequency and a small cover, clonal fragments were not excavated. Whenever possible, the parameters of the clonal growth of these species were estimated on the basis of the plants available in the herbarium of the Institute of Zoology and Botany of the Estonian Agricultural University. The herbarium plants were measured only in case they had been collected from similar communities. For 39 species out of 166 found in the vegetation samples, it was either impossible to measure all parameters of clonal propagation, or else sample size was too small (< 5). In each 1 m^2 plot the total cover for these species constituted less than 5%. The parameters of clonal propagation for these species were treated as the missing values (pair-wise deletion) in data processing.

Data analysis

The analysis of the data comprised three major steps. Firstly, we calculated the community-wide characteristics of clonal growth (Table 2). For each plot, we calculated the weighted average of each clonal growth parameter (M_{pj}) as:

$$M_{pj} = \Sigma\ a_i\ p_{ij} \tag{2}$$

Here a_i is the cover (ranging from 0 to 1) for the species i in the plot and p_{ij} is the value of the j-th clonal growth parameter for the species i.

We measured the difference in extent of clonal mobility among the coexisting species with the coefficient of variation of the medians of rhizome increment for all species in one plot. The coefficient of variation was chosen as it is an estimate of variance independent of the value of the sample mean. To correct also for a possible bias associated with the differences in sample size, we used the following correction (Sokal and Rohlf, 1995):

$$\mathrm{CV}_{\mathrm{increment}} = (1 + 1/4n)(\mathrm{St.Dev}_{\mathrm{increment}} \times 100/M_{\mathrm{increment}}) \tag{3}$$

Here $\mathrm{CV}_{\mathrm{increment}}$ stands for the corrected coefficient of variation for median rhizome increment per plot, n is sample size, $\mathrm{St.Dev}_{\mathrm{increment}}$ is the standard deviation of rhizome increment for one plot, and $M_{\mathrm{increment}}$ is the mean of the rhizome increments for all species found in a plot.

Secondly, we estimated the effect of environmental conditions on the averages of clonal growth parameters, species density, and ramet density as well as the general differences between the communities in average clonal growth. To test for the general relationships between different environmental variables and vegetation characters (incl. community-wide parameters of clonal growth), we built a squared correlation matrix with the Pearson's r and probabilities of error (p-level). To correct for the mass effect we employed the Bonferroni type correction with the Dunn-Šidák method (Sokal and Rohlf, 1995) and obtained the critical p-level (experimentwise error rate) using the following equation:

$$p_{\mathrm{critical}} = 1 - (1 - 0.05)^{1/k} \tag{4}$$

Here 0.05 is the original level of probability of type I error and k stands for the number of comparisons below the diagonal of the squared correlation matrix. To obtain a normal distribution, the number of species per plot was square-root transformed prior to analysis.

The general linear mixed model as implemented in the procedure MIXED of the statistical package SAS (version 6.12, SAS Institute Inc., Cary) was used to estimate the impact of biomass, light availability, mowing regime, and site on species density, ramet density and community's clonal growth parameters. Due to the high association and lack of overlap between the factors *MOWING* and *SITE*, they were combined into a new factor named *HABITAT*. This factor had seven different levels: forest sites with no mowing, open sites with the mowing frequency 0.1 times/year, open sites with the mowing frequency 0.2 times/year, open sites with mowing frequency once a year, wooded meadow sites with mowing frequency 0.5 times/year, wooded meadow sites with the mowing frequency 0.6–0.7 times/year, and wooded meadow sites with the mowing frequency once a year. The following model was tested:

$$Y = \mu + a_1 HABITAT + a_2 L + a_3 L^2 + a_4 B + a_5 B^2 + a_6 LB \qquad (5)$$

Here Y denotes a dependent variable (species density, ramet density and community averages of clonal growth parameters), μ is the intercept, L stands for light penetration coefficient, B is biomass, and a_1–a_6 are the coefficients. The factor *SITE* was included in the model as a random factor. The factors L and B were nested in *HABITAT*, while the factors *SITE* and *HABITAT* were nested in community type. Type 3 test of fixed effects was used with the iterative Restricted Maximum Likelihood (REML) procedure to estimate the effect of the variance components. To test for the dependence of the variables on biomass, light availability and different mowing regimes within one community type, as well as for the differences in the average values of the variables between the three community types, we used the statement ESTIMATE. In addition, we calculated the differences in the least squares means, however, as these yielded similar results they are not presented here.

We also tested whether the three measured clonal growth parameters could discriminate between the studied community types. For this, we used discriminant analysis with the forward stepwise method of the statistical package *STATISTICA* (StatSoft, 1995).

Thirdly, we estimated the intrinsic (independent of environmental conditions) relationships between the community clonal growth parameters, ramet density and species density. For this, we calculated Pearson's partial correlation coefficients while light, biomass, their squared effects, and combined effect [i.e. all continuous factors included in the model (Equation 5)] were kept constant as the partial variables. This was done for the whole data set as well as for each of the three community types separately. To the obtained matrices of partial correlations, we applied a correction of the error rates as described above (Equation 4).

Results

We found that over two-thirds of the 36 calculated correlation coefficients between the environmental factors and the vegetation variables were statistically significant (Table 3). In all three studied communities, the clonal growth parameters were correlated with biomass (Fig. 1), light availability (Fig. 2), and ramet density. Only rhizome increment was correlated with species density (Fig. 3) and mowing frequency (both correlations were negative, Table 3).

There were only a few effects of the environmental factors on the studied parameters of the vegetation and on the average community clonal growth parameters. Ramet density was dependent on all factors included in the model (Table 4). Species density was significantly dependent only on *HABITAT*, although there was marginal dependency also on light availability and on interaction term of light and biomass (Table 4). Of the studied community-wide clonal growth parameters, only the effect of biomass on ramet life span was statistically significant ($F_{7,56} = 2.23, p < 0.05$). The marginal effect of the square of biomass ($F_{7,56} = 1.96$, $p = 0.077$) showed that this relationship is slightly non-linear. No other effects of fixed factors were detected. The random factor *SITE* and intercept were never significant.

When the differences in the effect of the environmental factors on the vegetation parameters where estimated within one community type, we detected the effects of mowing frequency, biomass, and light availability on ramet density at open sites (Table 5). We also found the biomass of the forest floor to positively affect average ramet life span and average rhizome increment in the community (Table 5, Fig. 1a, b). The only direct effect of the community type on the average values of the vegetation parameters and on the clonal growth characteristics was that at open sites shoot density proved to be higher than in the other community types ($|t_{56}| = 4.72$, $p < 0.0001$ for both comparisons).

To estimate the intrinsic relationships between the community averages of clonal growth, ramet density, and species density, we calculated the partial correlation coefficients given for the whole data set in Table 6. We found that all three community clonal growth parameters were correlated with each other and that the coefficient of variation of the rhizome increments of the coexisting species was negatively correlated with branching intensity. We also found a

Table 3. Correlation matrix of relationships between different community characteristics as estimated by Pearson's correlation coefficients (*r*). $CV_{\mathrm{increment}}$ is the estimate of the difference in extent of clonal mobility (coefficient of variation of rhizome increments) in coexisting species. All communities are analysed together, $n = 104$. Statistically significant *p*-levels (*p*) are in bold script. The critical experimentwise error rate $p_{\mathrm{critical}} = 0.0014$

	Living biomass of ground layer		Ramet density		Species density		Mowing frequency		Light penetration coefficient		Ramet life span		Rhizome increment		Branching intensity	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Ramet density	0.53	**< 0.001**														
Species density	0.13	0.186	0.28	0.004												
Mowing frequency	0.12	0.221	0.26	0.008	0.88	**< 0.001**										
Light penetration	0.60	**< 0.001**	0.83	**< 0.001**	0.23	0.017	0.19	0.052								
Ramet life span	−0.39	**< 0.001**	−0.56	**< 0.001**	−0.08	0.435	−0.03	0.735	−0.63	**< 0.001**						
Rhizome increment	−0.47	**< 0.001**	−0.66	**< 0.001**	−0.40	**< 0.001**	−0.37	**< 0.001**	−0.69	**< 0.001**	0.80	**< 0.001**				
Branching intensity	0.31	**< 0.001**	0.72	**< 0.001**	0.16	0.096	0.16	0.102	0.66	**< 0.001**	−0.59	**< 0.001**	−0.77	**< 0.001**		
$CV_{\mathbf{increment}}$	−0.11	0.272	−0.53	**< 0.001**	0.22	0.026	0.27	0.006	−0.45	**< 0.001**	0.39	**< 0.001**	0.24	0.013	−0.46	**< 0.001**

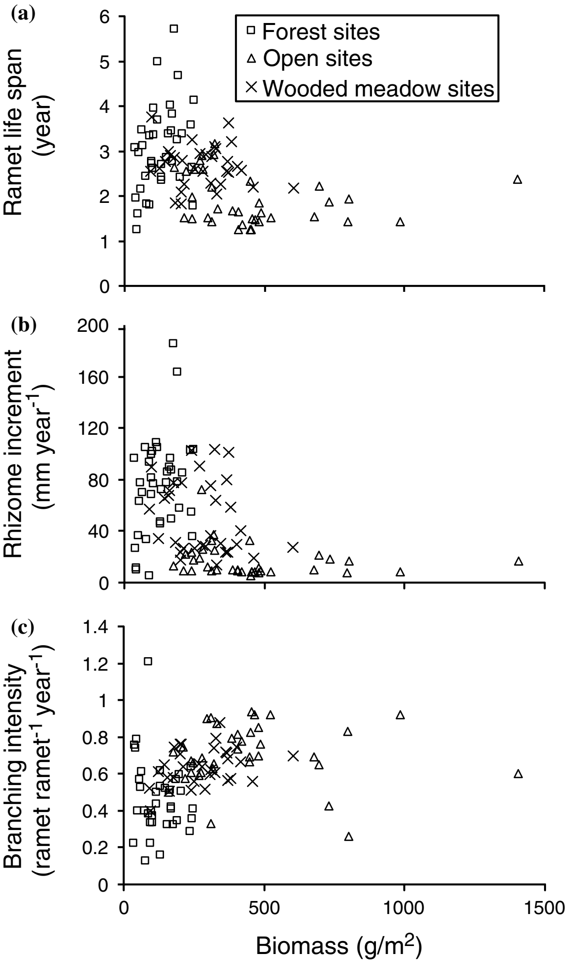

Figure 1. The average ramet life span (a), average rhizome increment (b), and average branching intensity (c) in different communities, plotted against plant living biomass of the herb layer of the community.

positive partial correlation between species density and ramet density, as well as between ramet density and branching intensity (Table 6).

When we analysed the three types of communities separately, we established a positive partial correlation between branching intensity and ramet density for forest sites ($r = 0.61$; $p = 0.0002$), and between ramet life span and species density for open meadow sites ($r = 0.56$; $p = 0.0014$). We also found a negative partial correlation between community vegetative mobility (rhizome increment) and species density for wooded meadow sites ($r = -0.54$; $p = 0.0036$). There was no statistically significant correlation between the coefficient of variation of the rhizome increments of the coexisting species and species richness, which indicates

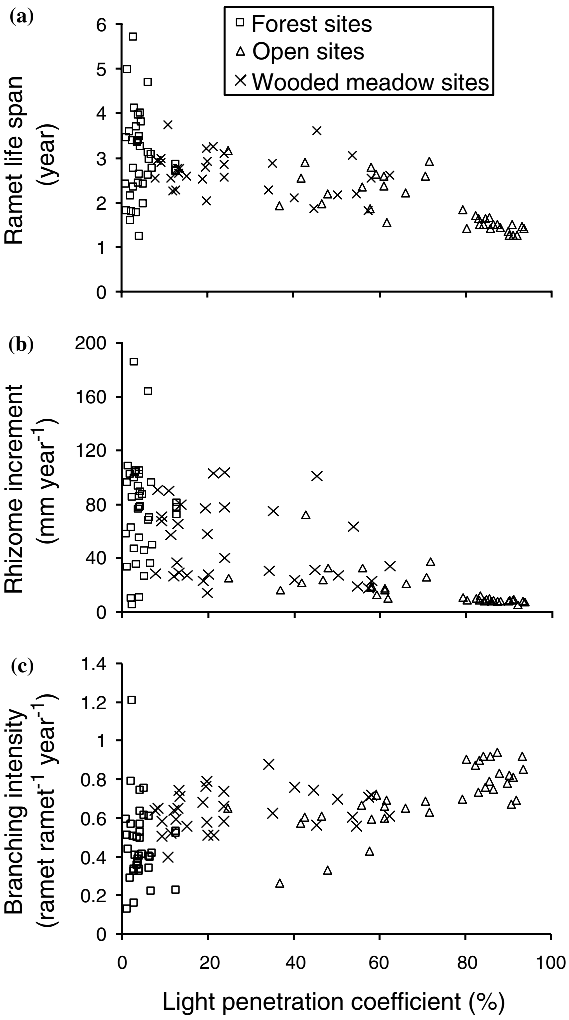

Figure 2. The average ramet life span (a), average rhizome increment (b), and average branching intensity (c) in different communities, plotted against light penetration through the tree layer.

that in the present case the more species-rich communities did not consist of species with more contrasting clonal mobility.

Discriminant analysis revealed that communities can indeed be discriminated on the basis of clonal growth (Fig. 4). Rhizome increment and branching intensity were included in the model, while the addition of ramet life span did not improve the predictive power of the model (Table 7). The first root (discriminant function) was in a very strong correlation with rhizome increment ($r = -0.95$) and was also correlated with branching intensity ($r = 0.69$). The second root was correlated with branching intensity ($r = 0.72$).

Discussion

General patterns and differences between the communities

Correlation between environmental factors, parameters of vegetation and clonal growth characteristics of community (Table 3) is to be expected as the environmental factors influence the composition of the vegetation, calculation of the community average of clonal growth depending on the latter. However, it is surprising that these relationships were not supported by analysis using

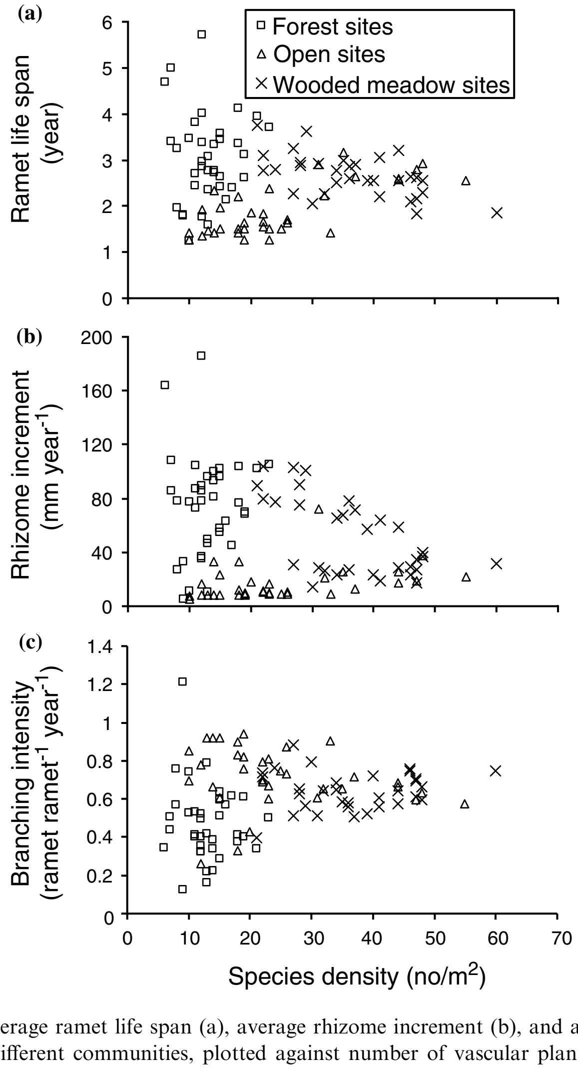

Figure 3. The average ramet life span (a), average rhizome increment (b), and average branching intensity (c) in different communities, plotted against number of vascular plant species in 1 m^2; plots.

Table 4. Type 3 effect of fixed factors of mixed model on ramet density and species density. *Habitat* is a combined factor for estimation of interactive effect of community type and mowing, *L* stands for the effect of light availability and *B* stands for the effect of biomass

Dependent variable	Factor	N. D. f.	D. D. f.	*F*	*p*
Ramet density	HABITAT	6	56	9.52	< 0.0001
	L	7	56	8.88	< 0.0001
	L^2	7	56	10.46	< 0.0001
	B	7	56	6.23	< 0.0001
	B^2	7	56	4.01	0.0013
	*L*B*	7	56	7.84	< 0.0001
Species density	HABITAT	6	56	2.45	0.035
	L	7	56	1.97	0.076
	L^2	7	56	1.69	0.13
	B	7	56	0.58	0.76
	B^2	7	56	0.35	0.92
	*L*B*	7	56	1.89	0.088

Table 5. Effect of mowing, biomass and light availability on studied variables in different types of the communities. Students t-values with 56 degrees of freedom are presented with experimentwise error rate $p_{\text{critical}} = 0.05$. Statistically significant *t*-values are in bold script. $\text{CV}_{\text{increment}}$ is the estimate of the difference in extent of clonal mobility (coefficient of variation of rhizome increments) in coexisting species

Effect	Species density	Ramet density	Ramet life span	Rhizome increment	Branching intensity	$\text{CV}_{\text{increment}}$
Mowing on open sites	−0.4	**4.73**	−0.18	−0.08	−0.71	−0.09
Mowing on wooded meadow	0.53	1.58	0.16	0.24	0.25	−0.65
Biomass in forest	−0.65	0.24	**2.84**	**2.59**	−0.25	0.23
Biomass in open sites	1.04	**−4.08**	0.03	0.05	0.51	−0.35
Biomass in wooded meadow	−0.42	−0.74	−0.03	0.54	0.46	−0.32
Light in forest	−0.15	−0.11	−1.27	−1.19	0.2	−0.87
Light in open sites	−0.46	**4.74**	−0.17	−0.08	−0.71	−0.07
Light in wooded meadow	0.81	−0.54	0.05	−0.35	−0.31	0.09

Table 6. Pearson's partial correlation coefficients (*r*) between studied variables. The effect of 5 partial variables was excluded: light, biomass, their squared effects and combined effect. $\text{CV}_{\text{increment}}$ is the estimate of the difference in extent of clonal mobility (coefficient of variation of rhizome increments) in coexisting species. All communities are analysed together, $n = 104$. Statistically significant *p*-levels (*p*) are in bold script. The critical experimentwise error rate $p_{\text{critical}} = 0.0034$

	Ramet density		Species density		Ramet life span		Rhizome increment		Branching intensity	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Species density	0.44	**< .0001**								
Ramet life span	−0.09	0.360	−0.04	0.690						
Rhizome increment	−0.13	0.210	−0.17	0.084	0.81	**< .0001**				
Branching intensity	0.39	**< .0001**	0.23	0.024	0.34	**0.001**	−0.39	**< .0001**		
$CV_{\text{increment}}$	−0.26	0.010	−0.07	0.471	0.09	0.366	−0.02	0.819	−0.30	**0.002**

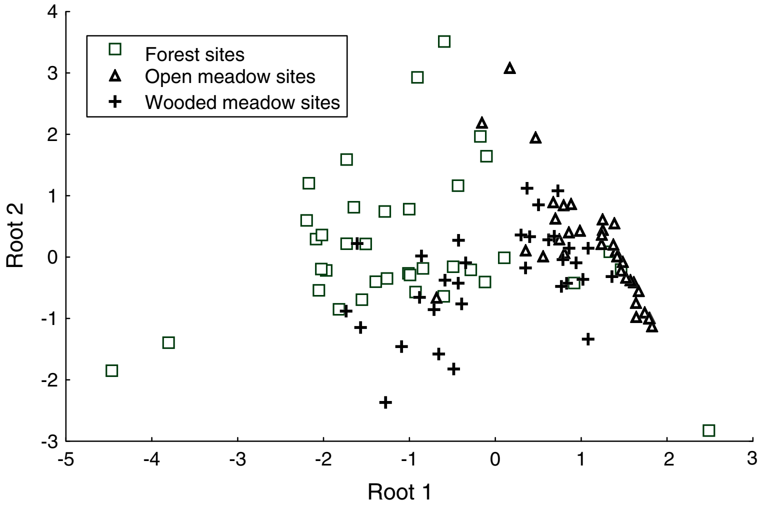

Figure 4. Distribution of individual vegetation analyses in the space of two discriminant functions. Root 1 is in strongest correlation with the average rhizome increment of the community while Root 2 is correlated with the average branching intensity in the community.

more sophisticated statistical methods. It is possible that we missed some important driving factor of the composition of these communities. Still, as the sites were characterised by very similar soil conditions and as light, being the most important above-ground factor, was also taken into account, it is more probable that variation within the individual sites, co-variation of different factors and the lack of the overlap of the latter in different community types created a situation where no effect of a single factor could be detected despite the occurrence of many putative relationships. This idea is also supported by the fact that there were hardly any statistically significant differences between the individual habitats or even between the three community types involved in this study. Yet the differences between meadow, wooded meadow and forest in the averages of the clonal growth parameters were remarkable (Table 2), even sufficiently large to enable discernment between the three community types (Fig. 4).

In our previous study of changes in community clonal growth after fertilisation (Sammul *et al.*, 2003) we found that fertilisation increased vegetative mobility in the community as well as branching intensity, although this result is dependent on the level of nitrogen limitation and the above clonal growth parameters increase most if N-limitation is strong. The productivity of the herb layer of the communities studied here is determined in a more complex manner, and both soil and light conditions influence it. We found that the increasing biomass of the herb layer in this study was negatively correlated with both the average vegetative mobility and the average branching intensity of the whole

Table 7. Discriminant function analysis summary. Three measured clonal growth parameters of community were grouped by type of the community. The models $F_{(4,200)} = 19.5$, $p < 0.0001$, and Wilkinson's Lambda = 0.518

	Wilks' Lambda	Partial Lambda	$F_{(2,100)}$ to remove	$F_{(2,99)}$ to enter	p	Tolerance	R^2
Variables in the model							
Rhizome increment	0.70	0.74	17.75		< 0.0001	0.813	0.187
Branching intensity	0.57	0.91	4.69		0.011	0.813	0.187
Variables not in the model							
Ramet life span	0.51	0.98		1.13	0.33	0.332	0.668

community (Table 3, Fig. 1). However, this is not a mere effect of productivity, as was shown by the analysis of a mixed model. Biomass co-varied with light availability and was influenced by mowing regime. Ultimately, this resulted in the differences between the communities and the individual sites (Tables 1–2).

We found that in the sequence meadow sites, wooded meadow sites, and forest sites there occurred a considerable increase in clonal mobility and a decrease in branching intensity in the community (Table 2). In meadows, extensive branching may be an effective way ensuring that the genet gains access to resources. There is no need to move around more than necessary for mere spreading and for avoiding interactions with stronger competitors, i.e. it is not directly necessary for survival of the genet. Branching also helps to avoid overtopping by other plants in meadows, as the height to width ratio of genet size can be reduced by increasing the number of ramets within the genet. In forests such strategy would be less profitable, as under trees it is vital to find a spot with sufficient available light. At forest sites and at wooded meadow sites light conditions are very heterogeneous. In general, species with plastic growth, capable of changing their clonal growth pattern in time and space (i.e. with the ability to "forage", Slade and Hutchings, 1987; Sutherland and Stillman, 1988), should have an advantage in communities where the resources are located heterogeneously (Hutchings and Wijesinghe, 1997). It can be concluded from many studies that the foraging behaviour of plants is mostly related to heterogeneity of light conditions (e.g. Dong, 1994; Hutchings and de Kroon, 1994; de Kroon and Hutchings, 1995). However, the effectiveness of morphological plasticity in foraging for open patches in the forest understorey has been questioned (Dong, 1994; but see Macdonald and Lieffers, 1993). Our results show that in wooded communities, where light is distributed highly heterogeneously, there are more species with higher mobility and longer ramet life span (see also Song *et al.*, 2002). It is possible that high absolute mobility values accord with high plasticity of mobility. However, even the ability to move over a large distance alone is advantageous for finding a suitable place below the shade of trees, considering the scale on which heterogeneity of light occurs in forested areas (see also Stuefer, 1996). Regardless of foraging ability, the growth form which allows ramets to move long distance vegetatively during their first year of life and then inhabit a chosen spot for a long time seems to suit well into the forest environment where the light gaps are spatially separated but last relatively long.

Relationship between clonal mobility and species richness

There is not much information available yet on how clonal mobility may influence species interactions. Almost always the species which take an advantage of undisturbed competition and changing environmental conditions are clonal (e.g. Bobbink and Willems, 1987; Soukupová, 1992 and references therein). Yet the most species-rich communities also consist mainly of clonal species (Kull and Zobel, 1991; Kukk and Kull, 1997; Cantero *et al.,* 1999; Klimeš *et al.,* 2001). It has been hypothesised that if the inferior competitor is mobile it may avoid competitive exclusion by moving to a more favourable spot and hence contrasting mobility of species may enhance their coexistence (Schmid and Harper, 1985). In this study we found no evidence supporting the hypothesis that the species coexisting at more species-rich sites have more contrasting clonal mobility compared with species coexisting at less species-rich sites. Nor did we find any general direct relationship between species density and community clonal growth. However, we established relationships differing in different types of communities.

Let us assume for a moment that high species density is a normal situation for a calcareous dry boreo-nemoral meadow (Kull and Zobel, 1991; Kukk and Kull, 1997). This high species density is the result of many co-varying factors: low productivity, low acidity, traditional management, etc. In this case both wooded meadows and open meadows have similarly low clonal mobility in the community and a medium life span of ramets (Fig. 3). This may be ascribed to the averaging effect of having many species in the sample, being thus a statistical peculiarity that has no meaningful biological explanation. Let us assume now that for some reason species density starts to decline. This could be due to cessation of management, some disturbance, increase in productivity because of soil formation, or the fact that managers applied fertilisers, or some other reasons. It is a situation where the succession of wooded meadows and open meadow sites, which are otherwise quite similar, proceeds in different directions (see also Tamm *et al.,* 2002). In open meadows, average ramet life span in community decreases, as does also the clonal mobility of the community. In wooded meadows, however, species with longer ramet life span and higher mobility gain abundance. In the case of abandonment, the succession of these communities proceeds quickly toward forest and the composition of the clonal growth forms of the herb layer becomes more similar with the composition of the community of the forest floor. Thus, the negative intrinsic relationship between the community average of rhizome increment and species density in wooded meadows may indicate changes occurring in the vegetation after abandonment.

Relationship between ramet turnover and species richness

Decrease in species density usually means that a few species start to dominate. These species may have, although not necessarily, certain growth form (see also Sammul *et al.,* 2003). Dominant herbaceous plants commonly have either a tussock growth form, highly resistant to invasion of the inhabited patch by other species (e.g. *Molina caerulea* L.), or the capability for quick clonal spread and a uniform coverage of the area (e.g. *Brachypodium pinnatum* L., see also Cheplick, 1997; de Kroon and Bobbink, 1997; Suzuki and Hutchings, 1997; Herben and Hara, 1997; Humphrey and Pyke, 1998). The decrease in species richness in the open meadows studied here is associated with the increase in the abundance of tussock species. This is consistent with the decreasing speed of vegetative mobility in the community as well as with decreasing average ramet life span. A decrease in ramet life span in the community leads to an increase in speed of shoot turnover. However, it is not established here whether ramets are replaced by conspecific ramets or by ramets of other species. We believe that a well-documented and fast turnover of shoots in species-rich communities (van der Maarel and Sykes, 1993) may be as fast and as common also in species-poor communities (see also Herben *et al.,* 1994; Pärtel and Zobel, 1995; Klimeš, 1999). It is just masked by the replacement of the ramets by their conspecifics which can not usually be detected by counting the shoots only. Many tussock-forming plants have annual ramets (e.g. *Molinia caerulea*, *Deschampsia caespitosa* L.) and are hence characterised by high ramet turnover speed even inside the tussock. Still, as their high capability for vegetative reproduction, small length of rhizome branches, and consequent dense packing of ramets render them highly resistant to invasions and strong patch-holders, they become common dominants in undisturbed meadows. Thus, one can observe both decreasing vegetative mobility and increasing shoot turnover happening with decreasing species density in open meadows.

Contrary to the suggestion that ramet turnover may increase with increasing species richness, several findings indicate that quite often shoots of one and the same species inhabit a patch for several years in species-rich communities (Klimeš 1999) and that there may be a positive correlation between species richness and average ramet life span in the community

(Sammul *et al.,* 2003). Our current analysis shows that this result may depend on the type of studied community (Fig. 3A). We found that independently of the effect of the environment, there is positive relationship between species density and community average of ramet life span only for open meadow sites. However, while this relationship revealed basically no trend for forest, a trend but with an opposite direction was marginally significant for wooded meadows ($r_{\text{partial}} = -0.49$, $p = 0.0092$, $p_{\text{critical}} = 0.0057$), with the partial correlation coefficients being clearly different ($p < 0.0001$).

Conclusions

Our study indicates that there are quite large differences between temperate deciduous forest, wooded meadow, and open meadow in the way how species richness and the community averages of the clonal growth parameters are related. While it has been hypothesised on several occasions that clonal mobility should increase the number of coexisting species (e.g. Sykes *et al.,* 1994), our results show that this might apply only to open meadows, where we found an increase in vegetative mobility with increasing species density. However, independently of the effect of environmental factors, clonal mobility and species density were, on the contrary, even negatively correlated for wooded meadow. The difference between the communities was also found regarding ramet turnover and, again, a positive relationship occurred between average ramet life span in the community (inversely related to ramet turnover) and species richness (Sammul *et al.,* 2003) only for open meadow. We did not find evidence for the hypothesis that more species-rich communities might consist of species with more contrasting clonal mobility. Thus, we found no clear support to any of the hypothesised relationships between clonal growth of the community and species richness. Instead, this study shows that the relationships between species richness and clonal mobility or ramet turnover might be strongly community-type specific. The differences between communities regarding the relationships between clonal growth, environmental conditions, and community structure deserve further attention.

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