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6 **Spatial Pattern and Temporal Dynamics of Bryophyte Assemblages in Saline Grassland**

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16

17 **Abstract** Dynamics of bryophyte assemblages of saline grassland were studied in Hungary.
18 A survey was carried out in two permanent plots by annual sampling of 0.25-m² quadrats over
19 a nine-year period. The study investigated: *i*) the extent of spatial and temporal dependence of
20 the assemblages and individual species; *ii*) the turnover of individual species and its
21 relationship to life-strategy types and *iii*) the effect of annual weather conditions on species
22 performance.

23 One of the plots showed succession; the frequency of some perennial species increased, while
24 that of some short-lived species decreased; this process was independent of local weather
25 conditions. The other plot showed a non-directional fluctuation, which was partly related to
26 precipitation in winter and early spring. The spatial and temporal dependence of this
27 assemblage was low; many short-lived species had a high turnover in the studied community.

28 In stable periods, neutral dynamic processes characterize the bryophyte assemblages of the
29 studied saline grassland and the occurrences of species were more or less independent in
30 space and time. Short-lived species showed high fluctuations and were probably influenced
31 by weather conditions or other factors. However, the frequency of perennial species, which
32 were influenced by local conditions, could directionally change displacing the short-lived
33 ones during succession. The relationships between turnover and life-strategy types were
34 weak, both the group of colonist and shuttle species were dynamically heterogeneous. Longer

35 observations are needed for a clearer exploration of the relationships between vegetation
36 changes and weather conditions.

37

38 **Keywords** Dynamics; Mosses; Permanent plots; Spatial dependence; Succession

39

40 **Introduction**

41

42 The most widely used approaches for the exploration of community dynamics involve
43 chronosequences (space-for-time substitutions) and permanent plots (Pickett 1989; Prach and
44 Walker 2011). Long-term studies of permanent plots have shown that the pattern of
45 succession is much more complex than predicted by chronosequences (Pickett et al. 2001).
46 Both spatially and temporally, the finer scale of the vegetation dynamics is the substitution of
47 individuals, ramets or shoots as an inner process of communities driven by life-history
48 characteristics of species or fine-scale disturbances. These within-community dynamics were
49 first recognized by Watt (1947), and later studied in detail for grasslands (Herben et al. 1997;
50 Morgan 1998). In these communities, a very high turnover of ramets was detected, while the
51 frequency distribution of the species did not change at stand level (Herben et al. 1993ab;
52 Palmer and Rusch 2001). In the absence of coarse-scaled disturbance, the directional changes
53 in stand-level frequency distributions originate from modifications of these fine-scaled
54 dynamics (Herben et al. 1993a). A neutral model, called the carousel model, was established
55 for the substitution of ramets based on the relatively homogenous and nutrient-limited alvar
56 grasslands (van der Maarel and Sykes 1993; van der Maarel 1996). This model does not
57 assume that interactions occur between species; there is no niche limitation, all sites are
58 suitable for colonization. The turnover of different species is thus determined by their life-
59 history traits (life-time of ramets, colonization ability, etc.). In more fertile sites with higher
60 vegetation cover, the neutral carousel model is not applicable because of niche limitation and
61 negative interspecific associations (Herben et al. 1997; Morgan 1998). Based on turnover and
62 growth form characteristics, species can be classified into mobility types (Herben et al.
63 1993b; van der Maarel 1996).

64 For bryophyte assemblages, the turnover of ramets (shoots) is similar or exceeds that of
65 vascular plants in the same community (During and ter Horst 1985; During and Lloret 1996).
66 Like vascular plants, the life-history characteristics and growth form of bryophyte species can
67 largely determine their dynamic intensity. Life-strategy types are determined by the life span
68 of the gametophytes, reproductive allocation, spore size and frequency of vegetative

69 propagules (During 1979, 1992). Liverworts and short-lived acrocarpous mosses dispersed by
70 airborne propagules show higher turnover and lower persistence than perennial mosses
71 spreading by vegetative growth. Spatial pattern and frequency are influential: fine-grained
72 pattern and low frequency are positively related to turnover (During and ter Horst 1985;
73 Økland 1994; During and Lloret 1996). These population level characteristics can determine
74 the community-level dynamics of the assemblages: grasslands dominated by turf-forming,
75 short-lived acrocarpous mosses are more dynamic than forest floor or mire communities
76 dominated by weft-forming, perennial, pleurocarpous mosses. There are three sources of
77 bryophyte establishment during internal dynamics or regeneration after disturbances: *i*)
78 vegetative growth of the surviving or neighboring shoots; *ii*) regeneration from the soil
79 propagule bank (gemmae, tubers, spores, shoot fragments); *iii*) colonization by airborne
80 propagules (spores, gemmae). As a rule of thumb, spores are the main sources of long-range
81 dispersal (establishment of new populations), while gemmae and clonal growth are more
82 important in the maintenance of local populations (During and van Tooren 1987; Rydin
83 2009). However, the importance of these establishment types differs with species, and with
84 communities, and in the same community the scale of disturbance is also influential. In
85 grasslands, the gametophytes of short-lived species are permanently present on the ground
86 floor, so the establishment of spores or vegetative propagules is a common internal process. In
87 the bryophyte assemblages of forest floor, especially in boreal forests, the dominant species
88 create perennial wefts and the internal dynamics are characterized by their vegetative growth
89 (Rydgren et al. 2001, 2005). However, short-lived species are permanently present in the
90 diaspore bank, and become prominent during regeneration after disturbances of the upper
91 organic layer (Jonsson 1993). A considerable difference between assemblages of vascular
92 plants and bryophytes is that the role of interspecific competition is lower for bryophytes than
93 for vascular plants (During and van Tooren 1987; During and Lloret 2001; Rydin 2009;
94 Michel et al. 2012). Experiments have shown a competitive hierarchy among coexisting long-
95 lived perennial mosses. However, the effect of competition was weak and it did not lead to
96 exclusion under natural conditions (van der Hoeven 1999; Rydin and Barber 2001). While
97 negative density dependence has been a general rule in ecology, for bryophytes a positive
98 correlation was found between shoot density and the performance of species (During and van
99 Tooren 1987; van der Hoeven and During 1997; Rydin 2009).

100 This study was focused on the dynamics of bryophytes in saline grassland using long-term
101 observation of permanent plots. Because of the high proportion of short-lived species, the
102 good colonization ability of individuals by airborne propagules and the supposed low effect of

103 competition, it was hypothesized that the carousel as a neutral model is a good approximation
104 of this assemblage's dynamics. Both spatial and temporal autocorrelation were expected to be
105 relatively low, because of the high proportion of independent colonization events. The study
106 aimed to address the following questions: *i*) are there any trends in the dynamics of bryophyte
107 assemblages? *ii*) what is the extent of spatial and temporal dependence of the assemblages and
108 individual species? *iii*) how different are the species dynamically, and how are these
109 differences related to their life-strategy types? *iv*) are the changes of assemblages and species
110 related to annual weather conditions?

111

112 **Material and Methods**

113

114 ***Study Area***

115

116 The study area is located in the Great Hungarian Plain, between the Danube and Tisza rivers
117 in Kiskunság near Apaj village. Its geographical position is 47°5' N, 19°5' E, altitude is 100 m
118 a.s.l. Climatically, it belongs to the forest-steppe transition zone. Mean annual temperature is
119 10.3°C, mean temperature in January is -1.7°C, and in July 21.4°C. Annual precipitation is
120 520 mm, and the annual vegetation growth period is 206 days (Dövényi 2010). The saline soil
121 shows a transition from solonchak to solonetz, and soil texture is clay-loam. The groundwater
122 depth from the surface is 1.2–2 m. In the upper 40 cm of the soil, pH is 9–10, pNa (sodicity)
123 is 2–3. Electrical conductivity (salinity) is 0.6–1.2 mS/cm measured in 1 : 2.5 soil : distilled
124 water suspension, and the range represents the annual variation (Tóth 2010). Maximum
125 salinity occurs in the 30–40-cm layer (Tóth 2010).

126 The vegetation is classified as Pannonic salt steppes and salt marshes (Natura 2000 code
127 1530), a priority habitat under the European Union Habitats Directive (Council Directive
128 92/43/EEC, 1992). The study was carried out in two plots, 400 m apart. Plot 1 represents the
129 *Achilleo setaceae-Festucetum pseudovinae* Soó (1933) 1947 corr. Borhidi 1996 community,
130 and plot 2 the *Artemisio santonici-Festucetum pseudovinae* Soó in Máthé 1933 corr. Borhidi
131 1996 community (Borhidi 2003). In the spring of 2010, the dominant vascular cover in plot 1
132 was 90%. Dominant species were *Festuca pseudovina*, *Achillea setacea* and *Medicago*
133 *lupulina*. Bryophyte cover was 60%, dominated by *Brachythecium albicans* and
134 *Homalothecium lutescens*. In plot 2, the cover of vascular plants was 40% dominated by
135 *Festuca pseudovina*, *Artemisia santonicum* and *Plantago maritima*, and bryophyte cover was
136 30% codominated by many species. In plot 2, the relative elevation is a bit lower and the

137 soil's maximum salinity appears closer to the surface than in plot 1. The area is moderately
138 grazed by sheep; the management is controlled by the Directorate of Kiskunság National
139 Park.

140

141 *Data Collection*

142

143 The 10 m × 10 m plots were selected and permanently marked in 2002. Twenty-five 0.25-m²
144 quadrats were placed regularly in a grid of 2-m spacing within the plots. In each quadrat, the
145 presence of bryophyte species was recorded. The survey was repeated annually from 2002 to
146 2010, between 20th March and 20th April, depending on the phenology of the early spring
147 vegetation. Sampling followed the protocol for bryophyte assemblages in the Hungarian
148 Biodiversity Monitoring System, representing 50 localities of different habitat types (Papp et
149 al. 2005, 2006). Voucher specimens of each species occurring in quadrats of the annual
150 surveys were deposited in the bryophyte herbarium of the Hungarian Natural History Museum
151 in Budapest (BP). Climatic (monthly precipitation) data were collected at a climate station
152 located 25 km from the study site. Because the time of the survey was in early April, the
153 amount of precipitation from previous December to March was used as a potential
154 explanatory variable. Nomenclature followed Tutin et al. (1964–93) for vascular plants and
155 Hill et al. (2006) for bryophytes.

156

157 *Data Analysis*

158

159 Plot- and quadrat-level species richness and cumulative species richness were expressed as
160 descriptive statistics of the assemblages. The effect of plots and years on quadrat-level species
161 richness was analyzed using ANOVA with a hierarchical error structure as plots, quadrats and
162 years. Between-year differences within plots were compared using Tukey-HSD multiple
163 comparisons (Zar 1999). Plot-level species richness was compared using a paired *t*-test. The
164 relationship between quadrat-level species richness and winter–early spring precipitation was
165 measured with the Pearson correlation coefficient (Zar 1999).

166 General structure of the assemblages in different years was explored using Principal
167 Coordinates Analysis (PCoA) with plot-level frequency data evaluated using the Ruzicka
168 dissimilarity index (Podani 2000).

169 Spatial and temporal dependence of the assemblages were analyzed at quadrat level using
170 presence/absence data of species. Jaccard dissimilarity index was calculated between quadrat-

171 pairs, which is the binary version of the Ruzicka index, i.e., joint absences were not influential
172 (Podani 2000). Within both plots, pairwise compositional dissimilarities between quadrats
173 were expressed in two ways: *i*) within-year dissimilarities, calculating dissimilarity values
174 among the 25 quadrats of the same year (300 quadrat-pairs per year); *ii*) within-quadrat
175 dissimilarities, calculating dissimilarity values between the data of different years of the same
176 quadrat (the design is unbalanced, for each quadrat there was one observation for 8 year
177 differences, two observations for 7 year differences etc., altogether 36 observations per
178 quadrat, 900 observations per plot). In both cases, spatial (and temporal) dependence were
179 analyzed using the Mantel test, calculating correlations between the compositional
180 dissimilarity values and spatial (or temporal) distance values (Zuur et al. 2007). The
181 significance of the correlation was tested using Monte Carlo simulations permuting the spatial
182 (or temporal) distance matrices, using 999 permutations. In the case of spatial analysis, all
183 years were included for the calculation of the correlation coefficient, but instead of permuting
184 the whole spatial dissimilarity matrix, the same permutations of the (sub)-matrices were
185 carried out in each year separately. Similarly, for temporal analysis the same permutations
186 were applied in the temporal distance (sub)-matrices of each quadrat separately. In this way
187 the temporal autocorrelation was preserved in the analysis of spatial dependence and *vice*
188 *versa*.

189 Temporal changes of species were described by their frequency distributions in different
190 years. Spatial dependence and quadrat-level temporal dynamics of species were studied
191 quantitatively only in plot 2. Rare and very frequent species were excluded from the species-
192 level spatial and temporal analysis, the mean annual plot-level frequency of the studied
193 species was between 4 and 20 out of 25. Spatial dependence of the studied species was
194 expressed using the Geary's C index (squared-difference coefficient) in each distance class
195 (Geary 1954). This is a standardized semivariogram, with a range from zero to infinity; the
196 expected value without spatial dependence is 1, with 0–1 for positive, and >1 for negative
197 dependence. By randomly permuting the observed data, the variance of the statistics can be
198 estimated, and the significance of the difference between the observed and the expected value
199 was evaluated using a t-test (Rosenberg 2001). Although correlograms and variograms were
200 used mainly in spatial analysis, it can also be extended to temporal dynamics (Herben et al.
201 1995). In this case, spatial distance classes were substituted by "temporal distances" with
202 different time intervals expressed in years. The values of Geary's C at different temporal
203 distances express the temporal dependence (stability) of the species. In the case of one-year
204 differences, the mean annual turnover (sum of establishment and extinction events) and mean

205 annual frequency increment (difference between establishment and extinction events) were
206 expressed. Because these values are influenced by frequency, they were standardized by mean
207 annual frequency of the species. The relationship between annual frequency of the species and
208 winter–early spring precipitation was studied using Pearson correlation analysis.
209 SYN-TAX 2000 was used for PCoA ordination (Podani 2001), Passage 1.1 for Geary’s C
210 calculation (Rosenberg 2001), all other analyses were carried out by R 2.14.0 (R
211 Development Core Team 2011) using the packages “vegan” (Oksanen et al. 2011) and
212 “multcomp” (Hothorn et al. 2008).

213

214 **Results**

215

216 *Community-Level Characteristics*

217

218 Based on a plot-level estimation, both vascular and bryophyte cover directionally increased in
219 plot 1 during the studied period. This increment was from 60% to 90% for vascular plants and
220 from 20% to 60% for bryophytes. In plot 2, the estimated vascular cover (in spring) did not
221 change (40%), while bryophyte cover fluctuated between 20% and 40%. The mean annual
222 number of bryophyte records (summarized frequencies) in the 25 quadrats was 104 ± 29
223 (standard deviation) in plot 1 and 219 ± 38 in plot 2. The relative frequency of short-lived
224 species (including colonist, annual shuttle and short-lived shuttle strategy types) was 37% in
225 plot 1 and 70% in plot 2.

226 Species richness in plot 1 was lower than in plot 2, both at plot- and quadrat-level (Table 1,
227 Fig. 1). The mean quadrat-level species richness was 4.2 in plot 1 and 8.8 in plot 2, which
228 significantly differed (ANOVA, $F(1,48)=290.04$, $P<0.0001$). The effect of years within plots
229 was also significant (ANOVA, $F(8,384)=22.5$, $P<0.0001$). The mean plot-level species
230 richness values were 13.9 versus 16.0, respectively; the difference was not significant (paired
231 t -test, $t=1.12$, $d.f.=8$, $P=0.29$). The larger differences in quadrat-level species richness
232 indicated that the frequency distribution of species was more even in plot 2. In plot 1, there
233 was a directional decrease of species richness values both at quadrat- and plot-level from
234 2005 to 2010 (especially between 2005 and 2007), while in plot 2 the species-richness values
235 fluctuated without any trend (Table 1). The saturation of cumulative species-richness values
236 was relatively fast in both plots. Quadrat-level species richness values reached 90% of the
237 cumulative species richness in the fourth survey (in 2005) in both plots. Plot-level saturation
238 was a bit slower in plot 2; here three new species were found in the seventh survey in 2008.

239 In the fluctuating plot 2, the correlation coefficient between quadrat-level species richness and
240 winter–early spring precipitation was 0.54 ($P=0.13$, Fig. 1). The two variables fitted well
241 between 2006 and 2010, but this was not true for the first part of the study (2002–2003, 2004–
242 2005). In the successional plot 1, quadrat-level species richness did not show any relationship
243 with precipitation ($r=-0.30$, $P=0.44$), especially after 2005, and the decrease of species
244 richness and increase of bryophyte cover were uncorrelated with precipitation (Fig. 1).

245 Based on PCoA, a succession could be observed in the species composition of plot 1 (Fig.
246 2a). The explained variance of the first ordination axis was very high (74.9%), while the
247 second axis had much lower importance (8.2%). Species composition changed considerably,
248 mainly between 2004 and 2008. The frequency of *Homalothecium lutescens*, a perennial
249 pleurocarpous moss, increased, while some acrocarpous, short-lived bryophytes decreased
250 (*Barbula unguiculata*, *Bryum dichotomum*, *Dicranella howei*, *Phascum cuspidatum*,
251 *Pseudocrossidium hornschuchianum*, Table 2). These processes caused the decrease of
252 quadrat-level species richness during this period. In plot 2, the changes seem to be
253 fluctuations rather than succession (Fig. 2b). The explained variances of the first two axes
254 were similar (34.8% and 27.8%, respectively), and cumulatively they explained a smaller part
255 of the total inertia than in the case of plot 1. Especially the species composition of 2003 and
256 2007 differed from other years. In 2003, the frequency of *Barbula convoluta*, *Bryum*
257 *caespiticium* and *Syntrichia ruralis* was considerably lower than in other years, while *Bryum*
258 *radiculosum* had an intermediate frequency in this year, and was practically zero in other
259 years (Table 3). In 2007, *Bryum dichotomum*, *Microbryum davallianum* and *Protobryum*
260 *bryoides* showed lower frequency than in other years. The temporal changes of frequencies
261 seem to be fluctuations in the case of most species, only the frequency of *Abietinella abietina*
262 showed a directional decrease, while *Bryum dichotomum*, *Pleurochaete squarrosa* and
263 *Pseudocrossidium hornschuchianum* increased in frequency with time.

264 The mean within-year Jaccard dissimilarity values of quadrat pairs were 0.50 ± 0.21 (s.d.) in
265 plot 1 and 0.42 ± 0.16 in plot 2 (Fig. 3). The within-year dissimilarity values slightly increased
266 with geographical distance in both plots (Fig. 3). The spatial dependence was stronger in plot
267 2 than in plot 1. In plot 1, the correlation between Jaccard dissimilarity values and spatial
268 distances was 0.084 (Mantel test, $P<0.05$); in plot 2 it was 0.138 (Mantel test, $P<0.001$).

269 The mean within-quadrat dissimilarity value was 0.54 ± 0.24 (s.d.) in plot 1, which showed a
270 significant temporal dependence; its correlation between temporal distance was 0.42 (Mantel
271 test, $P<0.001$, Fig. 4). In plot 2, the mean within-quadrat dissimilarity value was 0.47 ± 0.18
272 and it was independent from temporal distance; the correlation was 0.15 (Mantel test, $P>0.2$).

273

274 *Dynamics and Pattern of Individual Species*

275

276 The pattern and dynamics of individual species were studied only in plot 2. In plot 1, a
277 continuous directional change (succession) was found. The community dynamics did not
278 show directionality in plot 2, at least not over the period of the nine-year study. Plot 2 was
279 therefore more appropriate for the comparison of the individual inner dynamics of species
280 than the successional plot 1.

281 The occurrence of most species was spatially independent (*Brachythecium albicans*, *Bryum*
282 *dichotomum*, *B. caespiticium*, *Entosthodon hungaricus*, *Microbryum davallianum*, *Syntrichia*
283 *ruralis*), which means that their Geary's C values did not increase with geographical distance
284 and were not significantly lower than 1 in any spatial step in any of the nine years (data not
285 shown). For some species, Geary's C values were significantly below 1 in the shortest spatial
286 step (2 m) in one or two years out of the nine, and the index increased up to 4 m; these species
287 were *Abietinella abietina*, *Barbula convoluta*, *Bryum algovicum*, *Homalothecium lutescens*
288 and *Protobryum bryoides*. Only *Pleurochaete squarrosa* showed a characteristic spatial
289 dependence. Its C index was significantly below 1 in five years in the first spatial step and in
290 two years also in the second step, its C value increased with geographical distance up to 6 m.

291 A positive temporal dependence was observed at *Abietinella abietina*, *Barbula convoluta*,
292 *Brachythecium albicans*, *Bryum algovicum*, *Homalothecium lutescens* and *Pleurochaete*
293 *squarrosa* (Table 4). The C values of these species were significantly below 1 in one-, two-
294 and three-year differences. For other species, only the sequential years showed positive
295 dependences and there was no increasing trend in C values with years (*Bryum dichotomum*, *B.*
296 *caespiticium*, *Entosthodon hungaricus*, *Protobryum bryoides*, *Syntrichia ruralis*), or the C
297 values did not differ significantly from 1 at any temporal step (*Microbryum davallianum*). The
298 gametophytes of these temporally less-dependent species were short-lived, representing
299 colonist, annual shuttle and short-lived shuttle life-strategy types (Table 4).

300 For describing the annual dynamics of the species, the relationship between relative annual
301 turnover (sum of establishment and extinction events) and relative annual frequency
302 increment was evaluated (Fig. 5). An annual increment close to zero indicates that the
303 frequency of the species was more or less stable in the studied period. However, some short-
304 lived, acrocarpous species (*Entosthodon hungaricus*, *Bryum caespiticium*, *Protobryum*
305 *bryoides*, *Microbryum davallianum*) showed a relatively high turnover, which means high
306 fluctuations (many extinctions and colonization events) over time. The turnover of some

307 other, relatively long-term stable species was much lower (*Syntrichia ruralis*, *Homalothecium*
308 *lutescens*, *Barbula convoluta*, *Bryum algovicum*). *Bryum dichotomum* and *Pleurochaete*
309 *squarrosa* showed slight increases, while *Brachythecium albicans* and *Abietinella abietina*
310 exhibited a decreasing trend in the studied period.

311 Correlations between frequency and winter–early spring precipitation were significantly
312 positive only for a few species and are explained by the relatively short observation period
313 (Table 5). *Bryum dichotomum* and *Pleurochaete squarrosa*, two colonist species with
314 increasing frequency trend, and the relatively stable perennial *Homalothecium lutescens*, had
315 marginally significant, relatively high (>0.6) correlation with precipitation (Table 3, Table 5).
316 Both *B. dichotomum* and *P. squarrosa* had an increasing trend in two periods: between 2002–
317 2006 and 2007–2010; precipitation had a similar trend except for the low value in 2005
318 (Table 3, Fig. 1). Contrary to expectations, some species with increasing frequency trend
319 showed a stronger relationship to precipitation than the fluctuating species.

320

321 **Discussion**

322

323 *Mechanisms of the Dynamics of the Studied Assemblages*

324

325 Based on nine years of observations in plot 2, the carousel model seems to be a good
326 qualitative approximation of the dynamics of bryophyte assemblages of saline grasslands (van
327 der Maarel and Sykes 1993). The spatial dependence of the individual shoots was relatively
328 low, and their temporal dependence was not significant; practically all sites were available for
329 all species. The carousel model was developed through the long-term observation of species-
330 rich alvar vegetation, where the physical environment is homogeneous, with nutrient
331 availability limiting the performance of the species, leading to a neutral vegetation dynamics
332 (van der Maarel and Sykes 1993). The performance of the bryophyte populations in saline
333 grassland in the current study is also limited by high salinity, extreme water availability
334 variance within the year, and continuous grazing pressure (Tóth 2010). In early spring and
335 autumn the soil is water-saturated and the surface is partially flooded, while in summer the
336 upper layer of the soil is extremely dry. Water conditions also have considerable annual
337 variation depending on weather conditions.

338 However, spatial and temporal dependence of vascular assemblages of grasslands is much
339 higher than that of bryophyte assemblages. For vascular plants it has been shown that clonal-
340 growth is the major process for the establishment of new ramets (Herben et al. 1993b). The

341 matrix-building species belong to the sitter and phalanx mobility types according to Herben et
342 al. (1993b), or “constant” and “local” according to van der Maarel (1996). The gametophyte
343 of many short-lived bryophyte species was established from the propagule bank in the
344 assemblage of plot 2, and spatial dependence was lower in most cases than that of clonal-
345 growth. Therefore, many short-lived bryophyte species of this assemblage belonged to the
346 “pulsating” mobility type (van der Maarel 1996), for which spatial and temporal dependence
347 is low, and their frequency has high annual fluctuation. It is assumed that these species can
348 occur practically everywhere in the vegetation, but their establishment (germination) is very
349 sensitive to actual weather conditions. Therefore, a species could be a dominant member of
350 the assemblage in one year and rare in another. Because the main period for the performance
351 of these species is spring, when the soil surface is wet but not flooded, it was postulated that
352 winter and early spring precipitation is limiting their occurrence. This explanatory variable
353 was related to species richness of plot 2 in the second part of the observation period, however
354 the length of the study was too short for a more precise judgment of this relationship. It is
355 possible that this relationship is not linear. If this study period is drier than usual, it would
356 lead to a limited establishment of these species; if this period is extremely wet, it would be
357 also unfavorable.

358 In contrast, the example of plot 1 showed that the stage of vegetation characterized by neutral
359 dynamics, and dominance of pulsating species, is not necessarily stable for the longer term.
360 Perennial pleurocarpous mosses, such as *Homalothecium lutescens* in this case, could extend
361 by intensive clonal growth, thus displacing the short-lived acrocarpous species. The reason for
362 this expansion is not clear. It is possible that the grazing pressure decreased in this plot and
363 led to the accumulation of vascular litter and cover. These conditions are more favorable for
364 perennial pleurocarpous mosses than for the short-lived acrocarpous ones, which prefer more
365 open vegetation. Contrary to the fluctuations of plot 2, this trend-like successional change was
366 independent from annual weather conditions. A potential mechanism behind the changes
367 observed in plot 1 is interspecific competition. It is not obvious whether *Homalothecium*
368 extension, litter accumulation or the combination of these two factors caused a decline in
369 short-lived acrocarpous mosses. Most studies investigating the effect of interspecific
370 competition between bryophytes emphasize that its role is less important in community
371 organization than in the case of vascular plants (During and van Tooren 1987; van der
372 Hoeven and During 1997; During and Lloret 2001; Rydin 2009). However, most of these
373 experimental studies compared species of similar life strategy and growth forms, mostly
374 perennial pleurocarpous bryophytes or peat mosses (van der Hoeven et al. 1998; Malson and

375 Rydin 2009). In communities where perennial and short-lived bryophytes coexist, short-lived
376 species are restricted to special microsites, open patches and disturbed areas (Jonsson and
377 Esseen 1990; During and Lloret 1996; Rydgren et al. 2005). Short-lived mosses become
378 dominant only in those assemblages (as in plot 2) in which abiotic conditions or disturbance
379 pressure limits the performance of weft-forming species (Jonsson and Esseen 1990; Esposito
380 et al. 1999). The negative effect of vascular plant cover and litter on bryophyte cover and
381 species richness has been proven in many woodless habitats (mainly for meadows and
382 grasslands, Bergamini et al. 2001; Aude and Erjnaes 2005), while in the understory of forests,
383 positive interactions are also found between bryophyte and vascular layers (Márialigeti et al.
384 2009).

385

386 *Relationships between Dynamics and Life-Strategy Types of Species*

387

388 In many terrestrial bryophyte assemblages, the species turnover is related to their pattern and
389 frequency: subordinate or rare species showed higher turnover (dynamic intensity) than
390 dominant ones and species occurring in a fine-grained spatial pattern had higher turnover than
391 bryophytes that form large mono-dominant patches (Økland 1994; During and Lloret 1996;
392 Péntzes-Kónya 2006). This study partly supports this observation. The dynamics of individual
393 species of plot 2 was related to their pattern. Species showing the highest turnover
394 (*Entosthodon hungaricus*, *Bryum caespiticium*, *Protobryum bryoides*, *Microbryum*
395 *davallianum*) did not have spatial and temporal dependence, their pattern was fine-grained
396 with small isolated patches (shoots). However, this investigation's spatial scale was coarser
397 than most other bryological studies that focused on species pattern (During and Lloret 1996,
398 Péntzes-Kónya 2006). The relationship between turnover and frequency is not obvious. These
399 species were frequent (except *Entosthodon hungaricus*), they occurred in more than half of
400 the quadrats. However, their frequency had extremely high annual variance: in some years
401 they disappeared, in other years they occurred in almost all quadrats. The negative
402 relationship between frequency and turnover is characteristic only in those communities
403 where the dominant (matrix) species are weft building long-lived perennials and where the
404 occurrence of short-lived species is related to special microsites or disturbed patches (Økland
405 1994; During and Lloret 1996).

406 A strong connection was expected between life-strategy type and turnover of the species
407 because these categories also characterize their dynamics: perennial stayers have low
408 reproductive allocation and high gametophyte longevity, which result in low turnover, while

409 colonists and short-lived shuttle species are characterized by the opposite life-history
410 variables (During 1979, 1992). In plot 2, perennial stayers (*Abietinella abietina*,
411 *Brachythecium albicans*, *Homalothecium lutescens*) fulfilled these expectations: they had
412 relatively lower turnover and stronger spatial and temporal dependence than other species of
413 the assemblage. However, the results of plot 1 revealed their high dynamic ability by
414 vegetative growth expansion, which resulted in a directional change in the vegetation. The
415 higher turnover of colonist and short-lived shuttle life-strategy types are ambiguous. Most of
416 these species showed the expected results, but not *Pleurochaete squarrosa*, *Barbula*
417 *convoluta* and *Bryum algovicum*. These species had relatively low turnover and considerable
418 temporal (and for *Pleurochaete* also spatial) dependence. It is suggested that gametophyte
419 longevity of these species is greater than 2–4 years, which is characteristic of these strategy
420 types. Population biological studies have necessitated the revision of life-strategy categories
421 in some species, e.g., the annual shuttle category should be modified to short-lived shuttle for
422 *Phascum cuspidatum* because of the greater longevity of the gametophyte (Roads and
423 Longton 2003).

424

425 ***Practical Considerations***

426

427 Based on the present nine-year investigation, plot 1 showed succession while plot 2 showed
428 fluctuation. However, it is not certain if these dynamic processes are valid in the longer term.
429 It could be that the trend-like changes of plot 1 are also just fluctuations, but its cyclic period
430 is longer than the duration of the study. It is difficult to determine, based on this study,
431 whether the expansion of *Homalothecium*, resulting in the deterioration of the assemblage,
432 was a rare event with a long-term effect, or an occasional event (every 10–30 yr) occurring as
433 a longer term fluctuation. The recognition of trends and succession in communities dominated
434 by fluctuating species, which follows annual weather conditions, seems to be more difficult
435 than in communities dominated by more stable, perennial plants. The ambiguous recognition
436 of directional processes in ecosystems characterized by species of high turnover and
437 fluctuations should be taken into account when interpreting data from short-term monitoring
438 studies.

439

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450

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Table 1 Plot- (100 m²) and quadrat- (0.25 m²) level species richness and cumulative species richness values in different years. Quadrat-level species richness values significantly differed between years, letters representing pairwise differences. At quadrat level, mean species richness \pm standard deviation are indicated

Plot 1	Plot-level species richness	Plot-level cumulative species richness	Quadrat-level species richness	Quadrat-level cumulative species richness
2002	16	16	4.5 \pm 1.5 ^b	4.5
2003	18	22	4.7 \pm 1.7 ^b	5.7
2004	21	25	5.0 \pm 2.2 ^{bc}	7.2
2005	20	27	6.5 \pm 2.6 ^c	9.0
2006	13	27	4.3 \pm 1.6 ^{ab}	9.5
2007	11	28	3.1 \pm 1.2 ^{ab}	9.6
2008	10	28	3.2 \pm 1.4 ^{ab}	9.8
2009	9	28	3.2 \pm 1.2 ^{ab}	10.1
2010	7	28	3.0 \pm 1.0 ^a	10.2
Mean	13.9		4.2 \pm 2.0	

Plot 2	Plot-level species richness	Plot-level cumulative species richness	Quadrat-level species richness	Quadrat-level cumulative species richness
2002	16	16	8.3 \pm 1.9 ^b	8.3
2003	17	20	6.6 \pm 2.4 ^a	10.7
2004	16	20	9.5 \pm 2.9 ^{bc}	12.6
2005	15	20	10.2 \pm 1.4 ^c	13.5
2006	18	21	10.9 \pm 1.0 ^c	14.1
2007	12	21	6.4 \pm 1.7 ^a	14.2
2008	19	24	8.1 \pm 2.2 ^{ab}	14.6
2009	13	24	9.3 \pm 1.6 ^{bc}	14.8
2010	18	24	9.6 \pm 1.7 ^{bc}	15.2
Mean	16.0		8.8 \pm 2.4	

Table 2 Frequency (maximum value is 25) of different bryophyte species in plot 1

	2002	2003	2004	2005	2006	2007	2008	2009	2010	mean
<i>Abietinella abietina</i>	2	2	4	2	3	3	5	8	8	4.1
<i>Acaulon muticum</i>	0	0	1	0	0	0	0	0	0	0.1
<i>Barbula unguiculata</i>	20	19	18	19	15	1	4	1	1	10.9
<i>Brachythecium albicans</i>	23	22	22	23	25	25	24	25	25	23.8
<i>Bryum algovicum</i>	0	2	2	0	0	1	0	0	0	0.6
<i>Bryum caespiticium</i>	1	0	1	1	1	0	0	0	0	0.4
<i>Bryum capillare</i>	1	0	1	0	0	0	0	0	0	0.2
<i>Bryum dichotomum</i>	6	3	3	7	2	0	1	0	0	2.4
<i>Bryum radiculosum</i>	2	4	1	0	1	0	0	0	0	0.9
<i>Bryum ruderale</i>	0	0	4	4	1	0	0	0	0	1.0
<i>Dicranella howei</i>	4	2	3	3	0	0	0	0	0	1.3
<i>Didymodon vinealis</i>	0	0	0	4	0	0	0	0	0	0.4
<i>Drepanocladus aduncus</i>	23	24	24	24	22	16	14	14	13	19.3
<i>Entosthodon hungaricus</i>	1	0	2	7	0	0	1	1	0	1.3
<i>Homalothecium lutescens</i>	8	4	7	18	20	19	24	24	20	16.0
<i>Microbryum curvicolium</i>	0	1	0	0	0	0	0	0	0	0.1
<i>Microbryum davallianum</i>	0	2	1	0	0	0	0	0	0	0.3
<i>Microbryum floerkeanum</i>	0	2	0	6	0	0	0	0	0	0.9
<i>Phascum cuspidatum</i>	5	14	11	16	5	0	1	0	0	5.8
<i>Pleurochaete squarrosa</i>	0	0	1	1	0	1	0	0	0	0.3
<i>Protobryum bryoides</i>	2	0	2	3	0	0	0	0	0	0.8
<i>Pseudocrossidium hornschuchianum</i>	12	12	14	13	5	2	3	1	0	6.9
<i>Pterygoneurum ovatum</i>	0	1	1	0	0	0	0	0	0	0.2
<i>Rhynchostegium megapolitanum</i>	0	1	0	6	4	5	3	3	4	2.9
<i>Syntrichia ruralis</i>	2	1	3	3	4	3	0	3	4	2.6
<i>Tortula lanceola</i>	1	1	0	1	0	0	0	0	0	0.3
<i>Tortula modica</i>	0	0	0	0	0	1	0	0	0	0.1
<i>Weisia longifolia</i>	0	0	0	1	0	0	0	0	0	0.1

Table 3 Frequency (maximum value is 25) of different bryophyte species in plot 2

	2002	2003	2004	2005	2006	2007	2008	2009	2010	mean
<i>Abietinella abietina</i>	18	21	17	17	21	6	5	5	4	12.7
<i>Barbula convoluta</i>	18	7	21	18	22	15	22	24	18	18.3
<i>Brachythecium albicans</i>	22	7	17	17	18	11	13	6	7	13.1
<i>Bryum algovicum</i>	19	14	19	25	25	19	20	24	13	19.8
<i>Bryum argenteum</i>	0	0	0	0	0	0	2	0	0	0.2
<i>Bryum caespiticium</i>	18	1	17	13	13	24	7	20	23	15.1
<i>Bryum capillare</i>	0	0	0	0	0	0	1	0	2	0.3
<i>Bryum dichotomum</i>	6	2	16	15	19	3	24	24	25	14.9
<i>Bryum radiculosum</i>	0	10	0	0	1	0	0	0	2	1.4
<i>Bryum ruderale</i>	0	0	0	0	1	0	1	0	0	0.2
<i>Didymodon vinealis</i>	24	18	24	24	25	24	24	25	25	23.7
<i>Drepanocladus aduncus</i>	21	25	21	19	24	23	21	25	22	22.3
<i>Entosthodon hungaricus</i>	1	0	7	17	13	0	2	0	1	4.6
<i>Homalothecium lutescens</i>	13	23	16	16	19	18	17	20	21	18.1
<i>Hypnum cupressiforme</i>	0	3	0	0	0	0	0	0	0	0.3
<i>Microbryum curvicollum</i>	0	1	0	0	0	0	0	0	0	0.1
<i>Microbryum davallianum</i>	14	17	17	23	20	0	12	14	22	15.4
<i>Microbryum floerkeanum</i>	2	0	0	0	0	0	0	0	0	0.2
<i>Phascum cuspidatum</i>	1	0	1	0	1	0	0	0	0	0.3
<i>Pleurochaete squarrosa</i>	1	1	1	4	6	3	6	6	9	4.1
<i>Protobryum bryoides</i>	11	10	19	24	21	1	8	11	14	13.2
<i>Pseudocrossidium hornschurchii</i>	0	2	5	1	2	0	3	9	12	3.8
<i>Syntrichia ruralis</i>	18	3	20	21	21	13	14	20	19	16.6
<i>Tortella inclinata</i>	0	0	0	0	0	0	1	0	1	0.2

Table 4 Temporal dependence of different species in plot 2 expressed as Geary's C values in different time intervals (temporal distances) in year. Significance levels from the expected value of independence (1.00) are * – $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.001$. Sample size in different time intervals was 200, 175, 150, 125, 100, 75, 50, 25, respectively. "ST" means life-strategy types according to During (1979, 1992), as P – perennial stayer, C – colonist, AS – annual shuttle, SL – short-lived shuttle

Species	ST	Time interval (year)							
		1	2	3	4	5	6	7	8
<i>Abietinella abietina</i>	P	0.70***	0.68***	0.77**	1.07	1.05	1.22	1.19	1.19
<i>Barbula convoluta</i>	C	0.76**	0.71***	0.75**	0.79*	0.84	1.02	1.07	1.07
<i>Brachythecium albicans</i>	P	0.73***	0.75**	0.74**	0.86	1.04	0.85	1.12	1.12
<i>Bryum algovicum</i>	SL	0.87	0.82*	0.74**	0.94	0.99	1.08	0.96	0.96
<i>Bryum dichotomum</i>	C	0.84*	0.93	1.14	0.64***	1.01	1.35**	1.69***	1.69***
<i>Bryum caespiticium</i>	C	1.17*	0.90	0.80*	1.18*	0.77*	1.11	1.33*	1.33*
<i>Entosthodon hungaricus</i>	SL	0.77**	1.14	1.44***	1.33***	0.87	0.49***	0.13***	0.13***
<i>Homalothecium lutescens</i>	P	0.87	0.75**	0.73**	0.83	0.80*	1.0	0.75	0.75
<i>Microbryum davallianum</i>	AS	0.97	1.04	1.10	0.99	0.82	0.90	0.80	0.80
<i>Pleurochaete squarrosa</i>	C	0.54***	0.51***	0.67***	0.72**	0.69**	0.97	1.09	1.09
<i>Protobryum bryoides</i>	AS	0.83*	0.98	1.24**	0.96	0.92	0.88	0.96	0.96
<i>Syntrichia ruralis</i>	C	0.76**	0.91	0.89	0.75**	0.66***	0.83	0.97	0.97

Table 5 Correlation between the frequency of bryophytes in plot 2 and annual winter–early spring precipitation (from December to March) and associated significance values

Species	<i>r</i>	<i>P</i>
<i>Abietinella abietina</i>	-0.17	0.662
<i>Barbula convoluta</i>	0.34	0.365
<i>Brachythecium albicans</i>	-0.44	0.240
<i>Bryum algovicum</i>	-0.04	0.915
<i>Bryum dichotomum</i>	0.69	0.039
<i>Bryum caespiticium</i>	0.06	0.884
<i>Entosthodon hungaricus</i>	0.09	0.813
<i>Homalothecium lutescens</i>	0.61	0.082
<i>Microbryum davallianum</i>	0.46	0.215
<i>Pleurochaete squarrosa</i>	0.64	0.065
<i>Protobryum bryoides</i>	0.34	0.363
<i>Syntrichia ruralis</i>	0.26	0.501

Fig. 1 Temporal changes of quadrat-level mean species richness (plot 1 open circles, plot 2 filled circles) and winter–early spring precipitation (crosses)

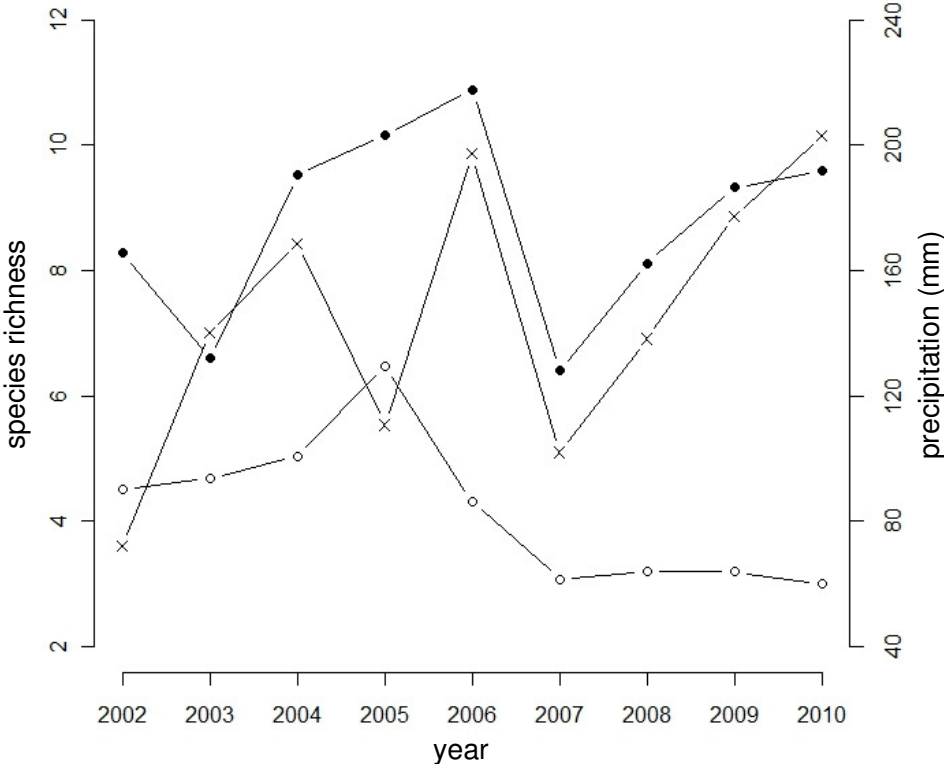


Fig. 2 Principal coordinates analysis (PCoA) of temporal changes in species composition for plot 1 **a** and plot 2 **b**. Explained variances in percentages are indicated below the axes, major annual transitions are indicated by trajectories

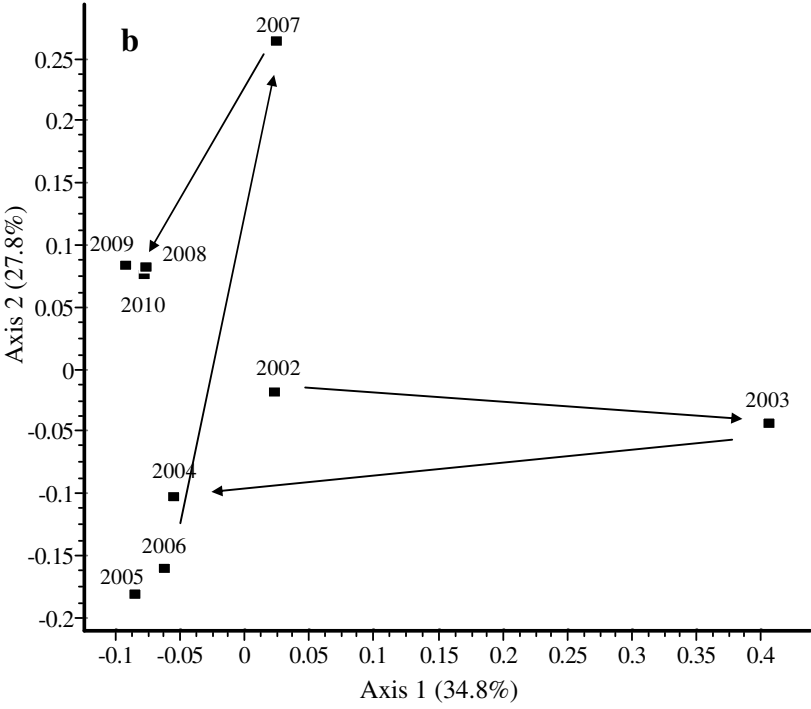
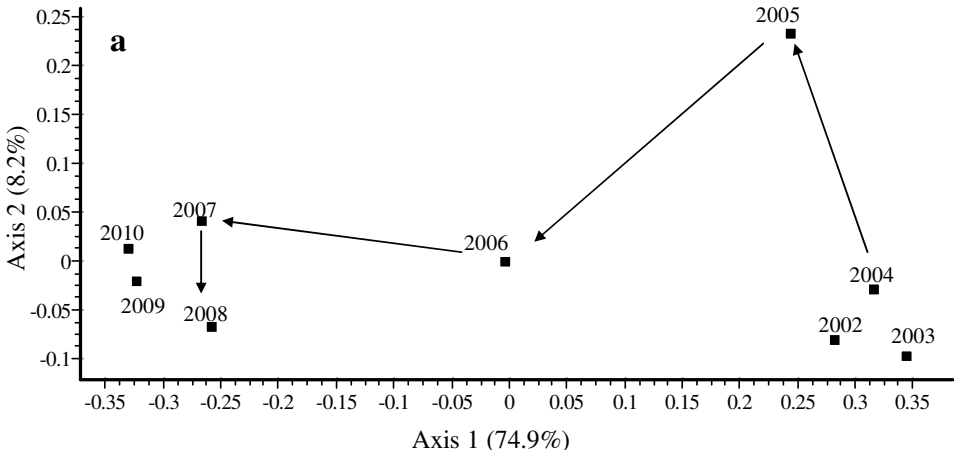


Fig. 3 Spatial dependence of species composition expressed as the mean Jaccard dissimilarity between quadrat-pairs at different spatial distances in the same year. Plot 1 is indicated by empty, plot 2 by filled circles, whiskers mean standard error

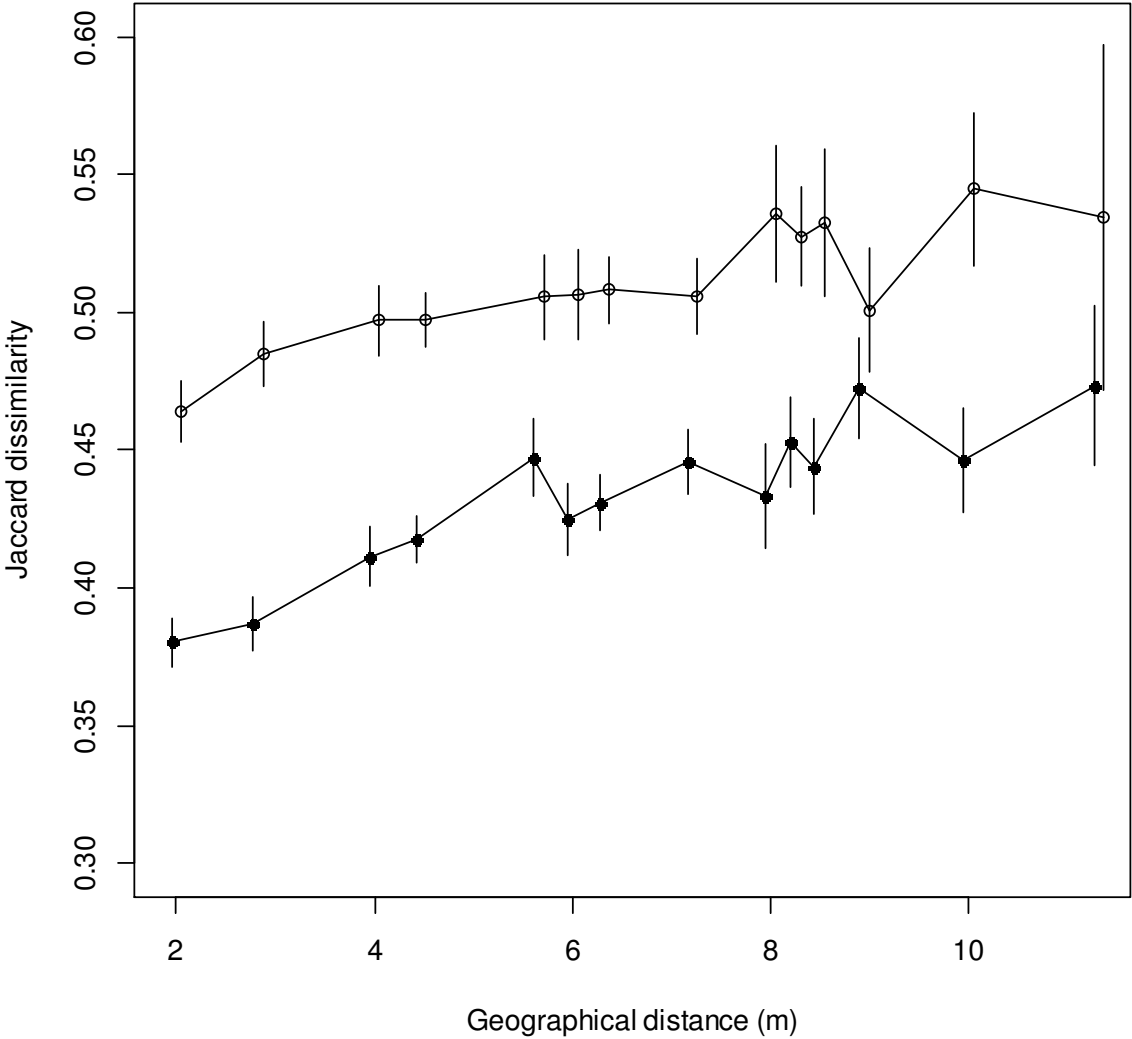


Fig. 4 Temporal dependence of species composition expressed as mean Jaccard dissimilarity between quadrat-pairs at different temporal intervals in the same geographical position. Plot 1 is indicated by empty, plot 2 by filled circles, whiskers mean standard error

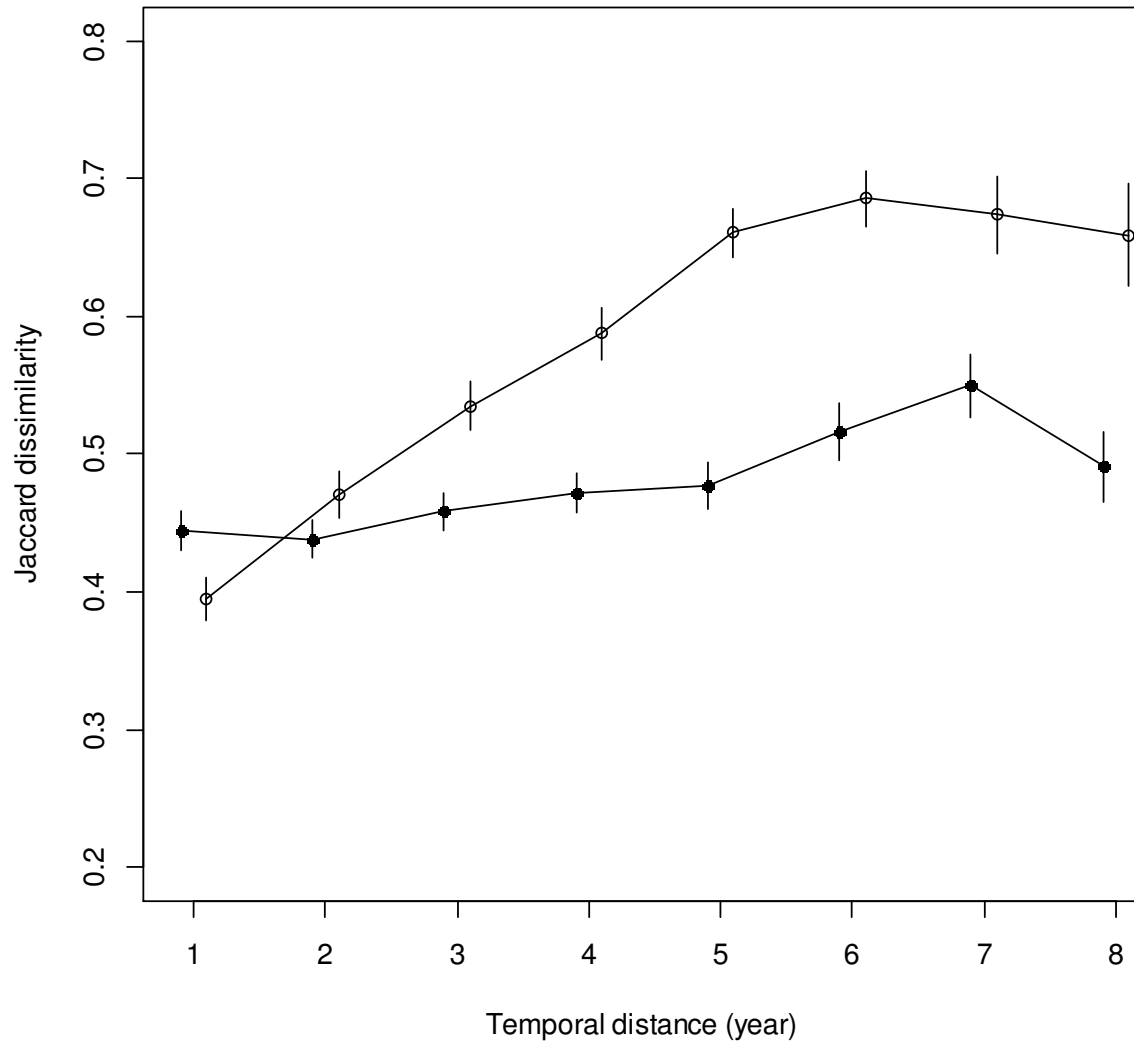


Fig. 5 Relationship between relative annual turnover (sum of annual establishment and extinction events divided by mean annual frequency) and relative annual frequency increment (difference between annual establishment and extinction events divided by mean annual frequency) of different species in plot 2. The species were abbreviated by the first three letters of the genus and the species names

