Species richness and species turnover in a successional heathland

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Abstract. Changes in species richness and species turnover during secondary succession following experimental disturbance were studied in eight permanent plots in a species-rich dry heathland in the southern part of the Czech Republic. The treatments applied were sod-cutting, burning, cutting of above-ground biomass, and control. The plots were sampled annually between 1992 and 2000; species richness was analysed at three scales, 25 cm × 25 cm, 1 m × 1 m, and 3 m × 3 m.

Disturbances resulted in increased species richness. The highest vascular plant richness was attained during the secondary succession after sod-cutting, where species established on exposed bare ground. Less severe disturbances by burning and cutting also caused a slight increase in the number of vascular plant species. For bryophytes and lichens, the highest increase in the number of species was also found in the sod-cut plots, where all cryptogams were removed by the disturbance. At the scale of 3 m × 3 m, species richness of both vascular plants and cryptogams peaked in 1995-1996, i.e. 3-4 yrs after the disturbance, and slowly decreased or slightly fluctuated without any trend thereafter. At smaller scales it either peaked later or constantly increased over the entire observation period of 9 yrs. Species mobility, expressed as species accumulation over time, was lower than reported from grasslands. Rates of species turnover, calculated as Jaccard dissimilarity between pairs of consecutive years, corresponded across different scales. This implies that successional dry heathlands have a higher small-scale mobility than heathlands which are apparently stable at larger scale.

Keywords: Burning; *Calluna vulgaris*; Cutting; Diversity; Plant community; Sod-cutting; Species mobility.

Introduction

Explanations for species coexistence in plant communities are often sought in the mechanisms whereby species avoid competitive exclusion. Disturbance is an important mechanism. Removal or reduction of biomass of superior competitors by disturbance reduces competition and allows for recruitment of less competitive species. In this way, species richness temporarily increases until the superior competitors regenerate (Grime 1973; Horn 1975; Connell 1978; Huston 1979, 1994, 1999; Glenn-Lewin & van der Maarel 1992; Palmer 1994).

Dry heathlands of western and central Europe, dominated by *Calluna vulgaris*, have historically developed under human-imposed disturbance regimes. Accordingly, their present existence depends on disturbances such as grazing, sod-cutting, burning or cutting (Gimingham 1972). *Calluna* is the superior competitor in heathlands, mainly due to its evergreen habit and production of slowly-decomposing litter, but its growth rate is rather slow (Gimingham 1960; Grime et al. 1988). Slow recovery of *Calluna* from disturbance implies that species-rich successional stages with an abundance of weaker competitors can exist for several years (Hobbs & Gimingham 1984).

Recent studies in grasslands provided evidence that vegetation which is apparently stable at larger scales, e.g. 10-100 m², shows considerable dynamics at smaller scales, e.g. < 0.1 m² (Herben et al. 1993a, b; van der Maarel & Sykes 1993; Sykes et al. 1994; Geißelbrecht-Taferner et al. 1997). These studies highlighted species mobility as a non-equilibrium mechanism responsible for the maintenance of high species richness by competition avoidance. As heathlands are generally less species-rich than grasslands, small-scale mobility is likely to play a minor role. In particular, ungrazed mature heathlands with a dense *Calluna* canopy and a continuous litter layer beneath provide very few gaps which could facilitate seedling recruitment and small-scale mobility. Higher mobility rates can presumably be expected only in early successional heathlands recovering from larger-sized disturbances, where gaps are more frequent or larger. This expectation, however, would contradict the results of Pärtel & Zobel (1995) who reported that in a successional series in Estonian alvar vegetation small-scale mobility was not correlated with the species turnover rate at larger scales.

The present study focuses on changes in species richness and species turnover in dry heathlands, regenerating after three types of disturbance, including sod-cutting, burning and cutting. Using data from a heathland management experiment (Sedláková & Chytrý 1999), we address the following questions:

1. How is the species richness in dry heathland affected by different types of disturbance?

2. Is there a unimodal relationship between species richness and time elapsed since disturbance?

3. Is there a correspondence between small-scale and large-scale species turnover?

Study site

The study site is located in a gently undulating heathland landscape near the town of Znojmo, southern Czech Republic (48° 49' N, 16° 01' E). The bedrock is formed of granite, covered with a nutrient-poor shallow soil. Mean annual temperature is about 8.8 °C and mean annual rainfall about 550 mm (Vesecký 1961). The heathlands are dominated by *Calluna vulgaris* and *Genista pilosa*, with frequent grasses and forbs such as *Avenula pratensis, Agrostis vinealis, Anthoxanthum odoratum, Hypericum perforatum, Hieracium pilosella, Asperula cynanchica, Pimpinella saxifraga, Rumex acetosella* s. lat., *Dianthus carthusianorum* s. lat., *Luzula campestris,* and *Carex humilis. Calluna* populations are uneven-aged, in the mature or degenerate phases (*sensu* Barclay-Estrup & Gimingham 1969), and have been rarely grazed in the 20th century. The details of the vegetation structure, history and management are summarized in Ambrozek & Chytrý (1990), Chytrý et al. (1997) and Sedláková & Chytrý (1999).

Methods

Field experiments and sampling

Temporal changes in species richness were evaluated as a part of the management experiment that included three types of disturbance: sod-cutting, burning and cutting above-ground vegetation. Vegetation was disturbed in 1992 and sampled yearly until 2000. The sampling scheme was originally designed in three replicated blocks, each with three treatments and the control, applied to plots of 3 m × 4 m to 4 m × 4 m. However, some plots were lost due to damaged markers early in the observation period, so we were only able to continue sampling in two sod-cut, three burned, two cut and one control plots. Therefore we refrain from statistical data analysis.

In sod-cut plots, vegetation, litter and topsoil were removed in April 1992. Before-treatment sampling was not done in these plots, as the original vegetation was totally destroyed by the treatment. The first sampling was done in July 1992.

Burning was performed in April 1992, creating a mosaic of bare ground and surviving vegetation patches. Original vegetation was sampled immediately before the treatment and the first after-treatment sampling was done in July 1992. In one of the three plots the original biomass of *Calluna* was higher than in the other two; therefore the fire was more intense there and the regeneration pattern differed to some extent (Sedláková & Chytrý 1999).

Cutting was done in July 1992 when the vegetation was in its phenological optimum. The plots were cut at 3-5 cm above ground and vascular plant biomass was removed, while litter, mosses and lichens were not affected. Original vegetation was sampled immediately before the treatment.

The control plot was first sampled in July 1992. All the plots were then repeatedly sampled in summer for eight subsequent years. Sampling included recording species composition in grids of 25 cm × 25 cm squares.

Data analysis

The data were first analysed separately for each plot. As the pilot analyses showed that the between-plot differences within one treatment were small, mean values from individual plots were averaged and presented together. This was also the case in burned plots which slightly differed in fire intensity.

Species numbers were counted separately for vascular plants and cryptogams (mosses and macro-lichens), in subplots of three sizes: 25 cm × 25 cm, 1 m × 1 m and 3 m × 3 m. For smaller subplots the counts were averaged over several subplots located on a grid within one basic permanent plot (pseudoreplicates), whereas the 3 m × 3 m subplot was only one within each permanent plot.

First, we counted the number of species (species richness) and cumulative number of species (cumulative species richness) in individual years. Species present in the original vegetation, sampled prior to the treatments, were not included in cumulative species richness counting. To estimate the rate of species mobility, we calculated the total species accumulation (van der Maarel & Sykes 1993; Sykes et al. 1994) which is the difference between species richness at time t and cumulative species richness in time $t + x$. In our case, the total species accumulation is the difference between the cumulative species richness in 2000 and species richness in after-treatment sampling in summer 1992. The maximum increase in species richness was calculated as a difference between the maximum species richness attained during the period 1992-2000 and the species richness in after-treatment sampling in summer 1992. Jaccard dissimilary in species composition between pairs of consecutive years was used as a measure of species turnover.
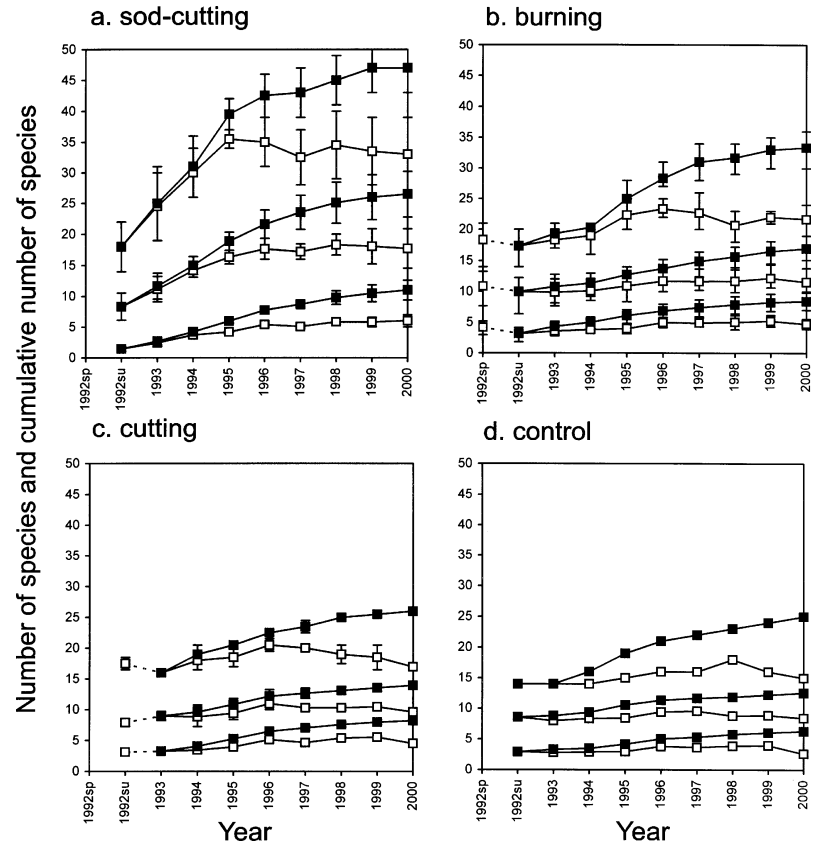
Fig. 1. Temporal changes in the number of vascular plant species (empty squares) and the cumulative number of species (full squares). Bars indicate range of values in different plots. 1992sp = spring 1992; 1992su = summer 1992. Records before and after treatments are connected by dotted lines. Lowest pairs of curves refer to subplots of 25 cm × 25 cm, central pairs 1 m × 1 m, and upper pairs 3 m × 3 m.
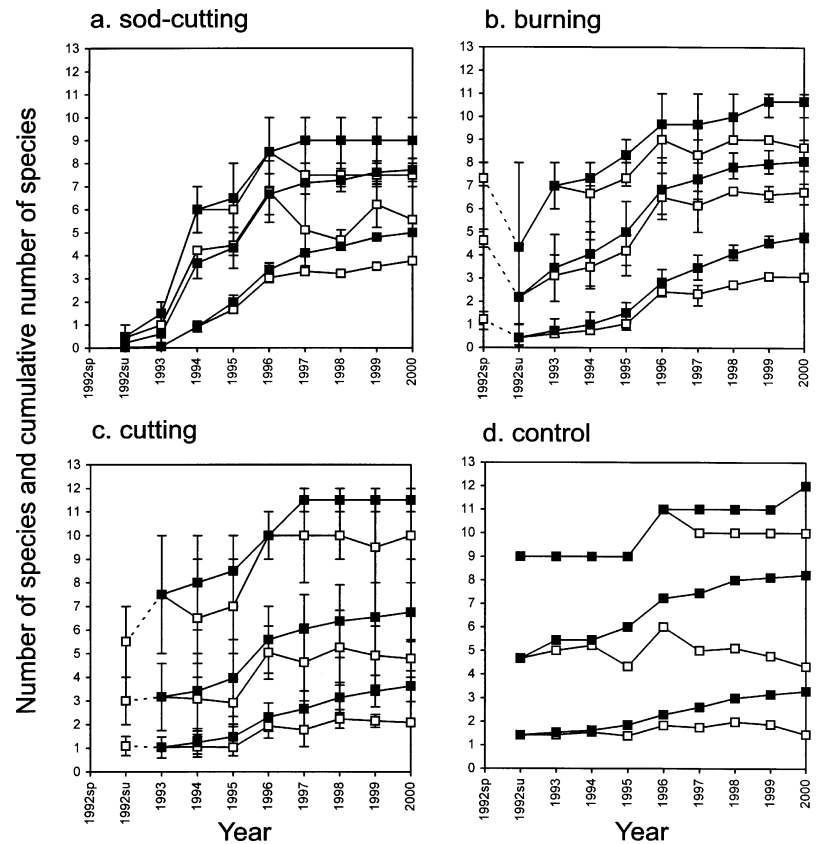
Fig. 2. Temporal changes in the number of cryptogam species (empty squares) and the cumulative number of species (full squares). Bars indicate range of values in different plots. 1992sp = spring 1992; 1992su = summer 1992. Records before and after treatments are connected by dotted lines. Lowest pairs of curves refer to subplots of 25 cm × 25 cm, central pairs 1 m × 1 m, and upper pairs 3 m × 3 m.

Table 1. Difference between species richness after disturbance in summer 1992 and maximum species richness attained during the period 1993-2000.

Plot size	25 cm × 25 cm	1 m × 1 m	3 m × 3 m
Vascular plants			
Sod cutting	4.6	10.0	17.5
Burning	2.1	2.2	6.0
Cutting	2.4	3.0	3.0
Control	1.0	1.0	4.0
Bryophytes and lichens			
Sod cutting	3.8	6.3	8.0
Burning	2.7	4.6	4.3
Cutting	1.1	2.0	4.5
Control	0.6	0.6	2.0

Table 2. Total species accumulation over the period 1992-2000. The values were calculated as the difference between cumulative species richness in 2000 and the number of species after disturbance in summer 1992.

Subplot size	25 cm × 25 cm	1 m × 1 m	3 m × 3 m
Vascular plants			
Sod cutting	9.6	18.2	29.0
Burning	5.3	7.0	16.0
Cutting	5.1	6.0	8.5
Control	3.7	4.0	11.0
Bryophytes and lichens			
Sod cutting	5.0	7.5	8.5
Burning	4.4	5.9	6.3
Cutting	2.5	3.8	6.0
Control	1.9	3.6	3.0

Results

During the study period, 1992-2000, both vascular plant and cryptogam species richness increased in all experimental plots including the control (Figs. 1 and 2). This increase was highest in the sod-cut plots, medium in burned and cut plots, and lowest in the control plot (Table 1). Species richness attained during the recovery from disturbance exceeded the pre-disturbance values. In all the plots, no weedy species occurred during the observation period, i.e. the increase in species richness was almost exclusively due to heathland and dry grassland species. Total species accumulation over this period generally decreased from sod-cut plots through burned and cut plots to the control, both for the vascular plants and cryptogams (Table 2).

At the scale of 3 m × 3 m, species richness of vascular plants in the sod-cut plots increased until 1995 (3 yrs after the disturbance), while the vascular plant richness in all the other plots and cryptogam richness in all the plots increased until 1996 (4 yrs after the disturbance). Later, species richness either levelled off (with some fluctuations) or slightly decreased. At the smaller scales of 1 m × 1 m and 25 cm × 25 cm species richness peaked later and in some plots the maximum was probably not reached 8 yrs after the disturbance took place.

Cumulative species richness did not considerably exceed the actual species richness during the first 2 yrs after the disturbance, indicating that establishment of new species was not accompanied by extinction of others (Figs. 1 and 2). In the following years the curves of cumulative and actual species richness diverged.

Inter-annual Jaccard dissimilarity, as a measure of species turnover, was generally high early after the disturbance in most treatments (Figs. 3 and 4). A reversed pattern was found in the control plot, where the turnover was rather low between 1992-1994, but increased after the dieback of several *Calluna* bushes between 1994-1995, which may be probably attributed to the disturbance caused by sampling. A striking fluctuation occurred between 1993-1994, when the turnover rate decreased in all plots, except for cryptogams in the sod-cut plot. All these trends were generally consistent across the scales of 3 m × 3 m, 1 m × 1 m and 25 cm × 25 cm.

Discussion

### Disturbance type and species richness

Reduced competition due to removal of dominant species is considered as the key mechanism causing the increase in species richness after disturbance (Connell 1978; Huston 1994). All disturbance types used in this study removed the *Calluna* canopy whereby competition, particularly for light, was strongly reduced. However, canopy removal alone little influenced species richness unless *Calluna* litter, moss mats and dense herbaceous vegetation were simultaneously removed and bare ground was exposed.

In cut plots, where no bare ground was formed by the disturbance, mainly vegetative regrowth of species already present occurred and very few new species appeared. Burning produced a heterogeneous environment consisting of a patchy mosaic of bare ground and resprouting vegetation. This heterogeneity, however, only slightly promoted the increase in species richness of vascular plants. The highest species richness of vascular plants was found in sod-cut plots where bare ground was exposed, despite the environmental patchiness being rather low there. This result seems to be in variance with the Environmental Heterogeneity Hypothesis (Palmer 1994) which predicts the highest species richness in the most heterogeneous environments. To explain this pattern, we have to consider the following:

a. sod-cutting   b. burning

c. cutting   d. control
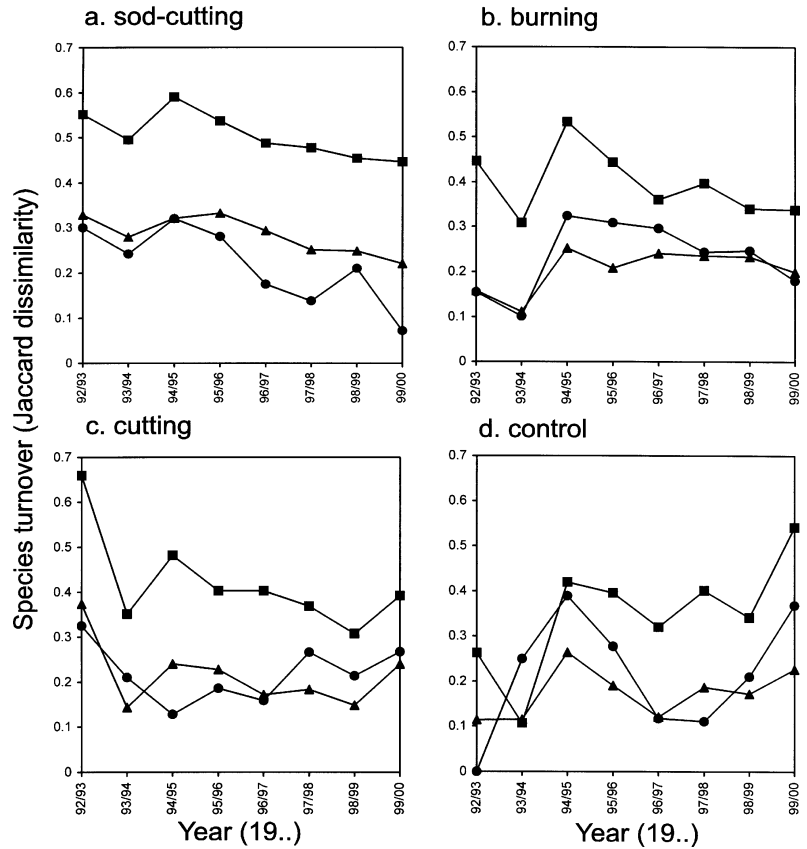
Fig. 3. Vascular plant species turnover expressed as Jaccard dissimilarity between pairs of successive years. Squares = subplots of 25 cm × 25 cm, triangles = 1 m × 1 m, dots = 3 m × 3 m.

a. sod-cutting   b. burning

c. cutting   d. control
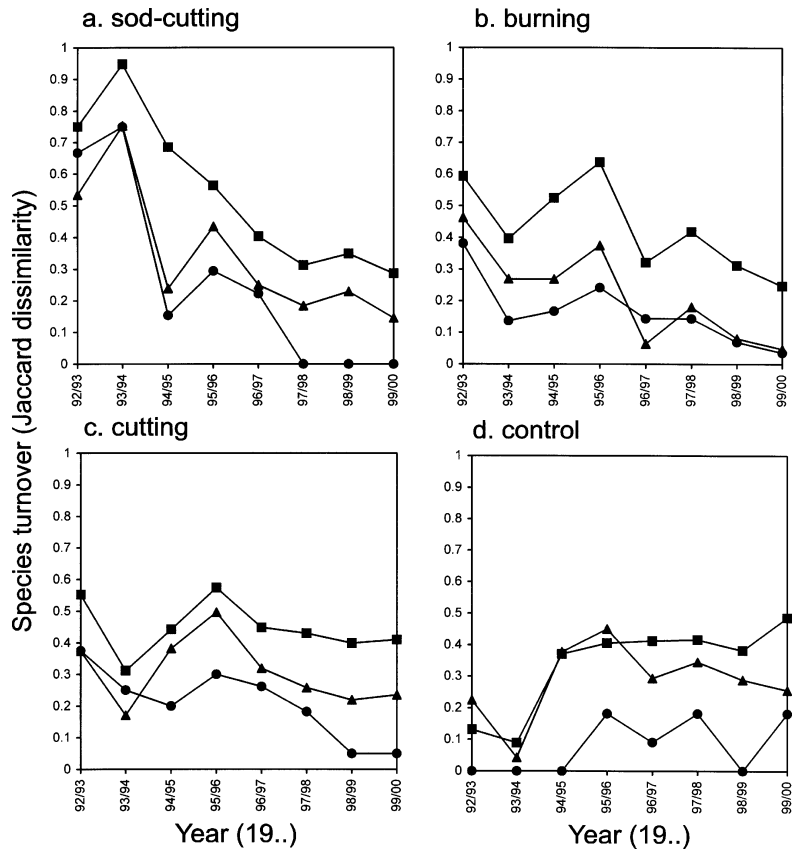
Fig. 4. Cryptogam species turnover expressed as Jaccard dissimilarity between pairs of successive years. Squares = subplots of 25 cm × 25 cm, triangles = 1 m × 1 m, dots = 3 m × 3 m.

1. There is a relatively large community species pool (*sensu* Zobel et al. 1998) in the studied heathlands. Using the data from previous phytosociological research (Ambrozek & Chytrý 1990; Chytrý et al. 1997) we estimate the size of the community species pool at ca. 70 vascular plant species.

2. The small size of disturbed patches (a few m²) imposes little restriction to the immigration of species from the surroundings.

3. The low growth rate of the superior competitor in poor soil results in a weak competition intensity during the first few years after the disturbance. This is particularly pronounced in the sod-cut plots, where the treatment caused an additional nutrient depletion.

In such conditions, the number of species in early succession is perhaps mainly dependent on the area of bare ground: the larger this area, the more species from the species pool colonize the patch by chance. In the burned plots, on the contrary, patches of surviving vegetation support less species than the adjacent patches of bare ground; in effect they only reduce the area available for species immigration from outside or recruitment from the seed bank. In addition, vegetation cover in the bare patches of burned plots regenerates faster than on the bare ground of sod-cut plots, and the early canopy closure prevents immigration of new species.

Species richness of cryptogams in sod-cut plots also dramatically increased from zero after the disturbance although it did not exceed the species richness of the other plots at the scale of 3 m × 3 m. However, it did exceed it at the scale of 25 cm × 25 cm. This indicates that for bryophytes and lichens, contrary to vascular plants, environmental heterogeneity can promote high species richness. In the heterogeneous environment of burned plots, cryptogamic synusia probably consist of those in unburned patches with late successional species such as pleurocarpous mosses or fruticose lichens, and those in burned patches which are colonized by early successional species such as small acrocarpous mosses. Sod-cutting exposes continuous areas of bare ground where the late successional species are eliminated and the diversity of cryptogamic synusia is consequently lower. The highest numbers of cryptogam species, however, were found in cut and control plots, which indicates that disturbance need not result in increased cryptogam richness in heathland.

Temporal changes in species richness after disturbance

Species richness of the studied heathland, measured in 3 m × 3 m subplots, generally increased during the first 4 yrs after the disturbance and mostly levelled off or slightly decreased thereafter. The Intermediate Disturbance Hypothesis (Connell 1978; Huston 1979) predicts that immediately after the disturbance species richness is low because few species from the species pool are able to colonize the plot. Species richness increases as new species arrive, but in later stages some of these species are outcompeted as the *Calluna* canopy closes. *Calluna* regenerates slowly, so the period of increased species richness is rather long. Hobbs & Gimingham (1984) reported increased species richness until about 15 - 17 yrs after fire in Scottish heathland, and a decline in the number of species thereafter.

The post-disturbance changes in species richness detected in this study are similar across the scales. The increase or decrease in species richness at one scale corresponds to increases or decreases at the other scales. However, species richness peaks earlier at larger scales (in 3 m × 3 m subplots usually after 4 yrs) than at smaller scales. Maximum species richness in 25 cm × 25 cm subplots was mostly found 6 yrs after disturbance and the cryptogam richness in sod-cut and burned plots increased until the end of the observation period. The earlier peak of species richness in larger plots is probably due to the fact that larger plots have a better chance of being colonized by most species from the species pool, just because they are larger. Within small squares, it takes longer for all species to reach almost all squares. It is to be noted in this context, that species mobility in the studied heathlands is much lower than that reported from grasslands. Total species accumulation in 50 cm × 50 cm squares over 4 yrs, reported by Sykes et al. (1994) from grasslands, is between 4.7 and 16.0, while corresponding figures in the studied heathlands over the first 4 yrs are 2.4 - 9.3, and over the second period of 4 yrs only 1.3 - 4.0. However, low species mobility in heathlands does not prevent species richness from increasing after disturbance: *Calluna*, the superior competitor, grows slowly and the competitive exclusion occurs later. The temporal pattern of species richness at the small scale indicates that competitive exclusion does not become the major driving force of the ecosystem before the sixth year after the disturbance.

Effect of scale on species turnover

There is much evidence from recent studies that ecosystems which are apparently stable at large scales are highly dynamic at small scales (Herben et al. 1993a; van der Maarel & Sykes 1993; Sykes et al. 1994; but see Klimeš 1999). The current heathland study enabled us to focus on the small-scale dynamics of a community which is dynamic also at a larger scale. In their study on successional alvar grassland and forest-floor vegeta-

tion, Pärtel & Zobel (1995) concluded that relatively stable and successional communities show a similar degree of small-scale dynamics. Our results are directly comparable to those of Pärtel & Zobel (l.c.) as we expressed the species turnover by Jaccard dissimilarity between the plots in two consecutive years, exactly in the same way as they did. We found a considerable difference in turnover between different years and different treatments, but there was a remarkable similarity between the scales. In other words, communities which were apparently stable at a larger scale also had lower species turnover at smaller scales, whereas communities with more dynamics at a larger scale showed higher turnover rates at smaller scales.

We suggest that in heathlands the small-scale species mobility is mainly dependent on the availability of bare ground. Therefore the large-sized disturbances through litter removal both trigger large-scale secondary succession and facilitate small-scale mobility. By contrast, in vegetation with a good litter decomposition, such as in grasslands, there is a constant recruitment of new individuals in small-scale gaps (Grubb 1977), and no large-sized disturbance is necessary to remove litter and facilitate species mobility. We hypothesize that such a mechanism is responsible for the fact that large-scale and small-scale dynamics can be correlated in heathlands but uncorrelated in grasslands.

Species richness and nature conservation

Maintenance of high species richness is often considered as one of the major goals of nature conservation. In vegetation management projects, however, it is necessary to control whether the increase in species richness is due to native species or due to unwanted species such as weeds or aliens. In the current study, all the species which newly appeared after the disturbance were natural constituents of the community, whereas synanthropic species were absent, probably due to poor soil and distant sources of diaspores.

In recent years, two competitive grasses, *Calamagrostis epigejos* and *Arrhenatherum elatius* have expanded into the dry grasslands and heathlands in our wider study area. The increased dominance is associated with a decline in species richness. The study plots were located on poor soils and they were not affected by these species. It was evident that sod-cutting, which produced nutrient-poor and drought-prone habitat, prevented expansion of these grasses. During our observation period, species-poor stands of *Calamagrostis* and *Arrhenatherum* developed in the immediate surroundings of one sod-cut plot, while short and open species-rich vegetation established inside. However, we observed a very good regeneration of *Arrhenatherum* in areas burned by accidental fires.

Our experiments were undertaken in plots of several m^2 and their results need not be valid if larger areas, such as several ha, are disturbed. We have no data on the origin of newly established species (i.e. whether they regenerated from the seed bank or immigrated from the surroundings), but it is possible that small plots have a higher influx of diaspores from their immediate surroundings than larger areas. It is therefore to be expected that the increase in species richness in large disturbed areas would probably be lower.

Most heathlands in temperate Europe are naturally poor in species and the maintenance of high species richness cannot be a conservation priority there. The *Carici humilis-Callunetum* community, analysed in this study, is a remarkable exception. It forms patchy mosaics with silicolous dry grasslands of the alliance *Koelerio-Phleion phleoidis* (*Festuco-Brometea*) and many dry grassland species occur there due to the mass effect (vicinism – see Zonneveld 1995). Past disturbances, e.g. grazing, accidental fires and soil erosion, were important factors in this community's history. They may have significantly contributed to the development of the present-day species-rich vegetation. Some kind of disturbance regime and maintenance of high species richness should therefore be an integral part of the present day management, practised by nature conservation authorities.

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