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Long-term effects of drainage on species richness of a fen meadow at different spatial scales

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Summary

Changes in species richness on a local scale are illustrated with an example of vegetation changes over 26 years in a species-rich fen meadow (*Calthion palustris*), which had been impacted by a deep drainage channel. The changes were monitored in the meadow as a whole and in 19 permanent plots situated in sites with various intensities of drainage. The similarity with an undisturbed local reference type of the hay meadow community was calculated for all plots and every year. After 26 years, the overall loss of species in the meadow as a whole (including all ditches) was less than 12%, while the overal loss in species in the permanent plots was 45%. Several species that declined in the permanent plots had survived in the ditches, while others, in particular sedges had migrated to low-lying areas. This example illustrates the need to survey changes in species richness on multiple scales.

Zusammenfassung

Die Veränderungen des Artenreichtums werden auf einer lokalen Skala am Beispiel der Vegetationsveränderungen in einer artenreichen Sumpfwiese (*Calthion palustris*) über 26 Jahre verdeutlicht, die von einem tiefen Entwässerungsgraben beeinflusst wurden. Die Veränderungen wurden für die gesamte Wiese und in 19 permanenten Probeflächen erfasst, die sich in Bereichen mit unterschiedlichen Entwässerungsintensitäten befanden. Es wurde die Ähnlichkeit mit einem lokalen, ungestörten Referenztyp einer Heuwiesengemeinschaft für jede Probefläche und jedes Jahr kalkuliert. Nach 26 Jahren war der gesamte Artenverlust in der Wiese als Ganzes (inklusive der Gräben) geringer als 12%, während der gesamte Artenverlust in den permanenten Probeflächen 45% betrug. Einige Arten, die in den permanenten Probeflächen abgenommen haben, überlebten in den Gräben, während andere, vor

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allem die Seggen, in die tiefer liegenden Bereiche abwanderten. Dieses Beispiel verdeutlicht die Notwendigkeit, Veränderungen des Artenreichtums auf multiplen Skalen zu erfassen.

Introduction

It is generally accepted that economic progress seriously damages biodiversity at all scales: from the habitat level up to the global biosphere (Ellenberg, 1978; UNEP, 1994). Until now there has not been much research focusing on the specific relation between changes in the socio-economic environment, translated in changes in land use, with consequences for the hydrological and physical conditions of the land, ending up in significant changes in biodiversity. Van Diggelen, Sijtsma, Strijker, and Van den Burg (2005), working at the scale of 1 km^2, related changes in land use and land use intensity with changes in frequency of 130 plant species in the northern part of The Netherlands in the period between 1930–1950 and 1970–1990. The authors found only a small net overall change despite large socio-economic and landscape changes. Most ecological species groups did not sharply react on changes in land use at that scale, although individual species showed marked changes (Witte, 1997). The explanation for this poor response on a scale of km^2 is that remnants of much larger populations had survived in ditch banks, road sides and in nature reserves.

On a local scale, changes in the abundance of species in plant communities—be it fluctuations or trends—can be indicative of the fate of the local populations. This type of information can largely be enriched by benefiting from synecological expertise derived from phytosociological research in general and long-term monitoring studies in particular (Müller, Rosenthal, & Uchtmann, 1992; Bakker, Marrs, & Pakeman, 2002).

The present paper will focus on the effects of land use changes on distribution patterns of wet meadow species at different scales. For this purpose we used a wet meadow, which was under the influence of drainage since 1975 and where vegetation changes had been monitored for 26 years in permanent plots. To explore the relation between local community-level processes (permanent plots) and larger-scale phenomena at the level of species and populations, we used species lists of the meadow of 1976 and 2003. Finally, we will pay attention to rare and characteristic species of well-defined plant communities, since they are believed to be most sensitive to changes in the environment at different scales.

Materials and methods

Site description

The meadow, in which the effects of drainage have been studied, is situated in the catchment of the Drentse Aa river in the northern part of The Netherlands at 53°01′N, 6°40′E and is about 0.7 ha (Fig. 1). A 2.5 m deep drainage channel has been dug alongside the meadow in autumn 1975, leading to a drop in the water table of 40–80 cm in the direct vicinity of the channel. High water tables were maintained close to the original stream due to the strong seepage intensity of groundwater (4 mm/day; Grootjans, Van Diggelen, Everts, Streefkerk et al., 1992) and the presence of a thick peat layer with a low permeability. It was estimated that a drop in water level of 10–15 cm had occurred close to the original stream. The vegetation of the meadow—classified in 1976 as *Senecioni-Brometum racemosii caricetosum nigrae* (alliance

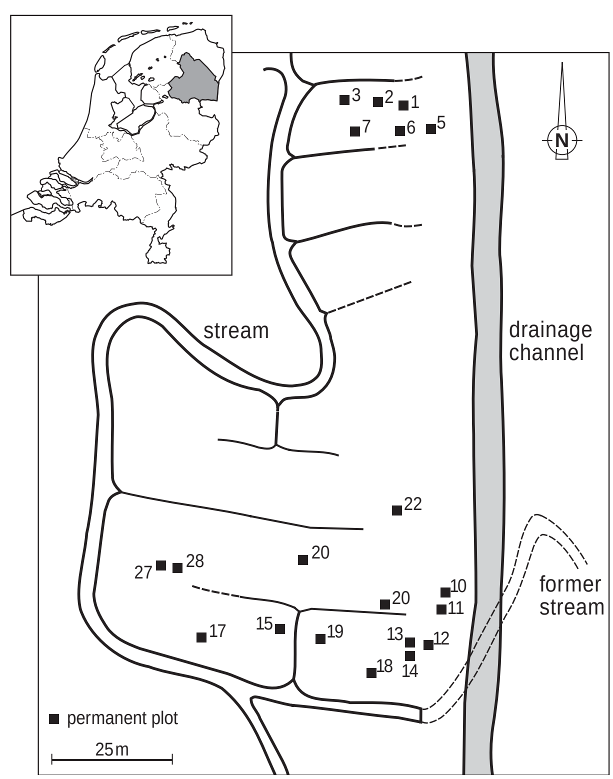

Figure 1. Map of the study area showing remnants of the meandering river enclosing the species-rich meadow. The deep drainage channel is present since 1975.

Calthion palustris)—was mown annually in June or July. In 1990/1991, the meadow was shortly grazed by sheep and not mown. At the end of the observation period 2000/2001, the meadow was abandoned and not mown.

Field sampling

The vegetation was first recorded in 1976 in 22 permanent plots of $2 \times 2\,m^2$, located in representative sites subjected to different drainage intensities. In the course of time, three plots were severely damaged and were discarded, leaving 19 plots which were used for analysis. They were recorded in 1976–1980, 1983, 1986, 1987, 1990, 1991, and 2001, using a cover-abundance scale (Londo, 1976). In May 1976 and 2003, the total number of species was counted in the whole meadow and surrounding ditches and streams.

The phreatic water table was measured from May to September 1977, using PVC piezometers with filters between 100 and 120 cm below the surface. The water table draw down for each quadrat was extrapolated from water table measurements during the summer in 16 sites.

Local reference type

Since we did not have information on the species composition of the meadow before the drainage activities, we compared the observed changes in meadow with undisturbed stands outside the influence of the drainage channel, which were situated in the same river valley and had experienced the same management for at least 10 years. The percentage similarity of all the relevés with a local reference of undisturbed *C. palustris* meadows was calculated. The reference type contained the regionally occurring character species of the *C. palustris* community and some differentiating species, which in the study area indicate the local differentiation in edaphic factors. Four character species of the alliance (*C. palustris*, *Lychnis flos-cuculi*, *Myosotis palustris* and *Lotus uliginosus*) and two differentiating species of the subassociation (*Carex nigra*, *Cynosurus cristatus*) occurred in the undisturbed reference type. Thirteen relevés were used to determine the local reference type. They have been obtained from Grootjans, Fresco, De Leeuw, and Schipper (1996) and can be regarded as an average situation of undisturbed hay meadows in the study area in space and time.

We calculated the percentage similarity with this local reference type to decide whether a local vegetation stand could no longer be considered to be part of the original meadow community in 1975. With respect to membership of the *C. palustris* community, we used the 20% similarity criterion: i.e., at 20% similarity with the local reference community that particular stand had lost community membership.

To calculate Percentage Similarity (Fresco, Van der Maarel, & Kazmierczak, 2001) we used

$$PS_{ij} = 100 \frac{\sum_k \min(y_{ki}, y_{kj})}{\min\left(\sum_k y_{ki}, \sum_k y_{kj}\right)},$$

where y_{ki} is the cover of the kth species at site i (j denotes the reference community). From the Percentage Similarity data, we used a linear regression analysis to determine the time at which the quadrates showed 20% similarity:

$$PS_i = a + bt.$$

Data analysis

Third-order polynomia were applied for the purpose of expressing the changes in cover of plant species during succession:

$$y_t = a_0 + a_1 t + a_2 t^2 + a_3 t^3,$$

where y is the estimated abundance and t is the time in years since the start of the recording in 1976. The percentage of annual species was calculated according to Hodgson et al. (2005). Rarity of species follows Van der Meijden, Odé, Groen, Witte, and Bal (2000).

Results

Change in frequencies of species

Among the character species, *C. palustris* was most persistent in the meadow, and remained present in 50% of the plots after 26 years. *L. uliginosus*, however, disappeared from all plots after 10 years. *L. flos-cuculi* also showed a dramatic decrease following the digging of the deep ditch, but it took more than 20 years before the species disappeared from all the plots (Fig. 2). In general, species with a low initial frequency (locally rare species) were the first to go (Table 1). Species, such as *Ranunculus lingua*, *Trichlogin palustris*, *Carex ovalis* and *Valeriana dioica* disappeared from the plots within 5 years. Some species with a low initial frequency, however, responded positively to drainage during the first

10 years (*Rhinanthus angustifolius* and *Poa pratensis*), but later on decreased again, both in frequency and cover. Another exception was *Dactylorhiza majalis*, which is a rare orchid species that maintained a small population along the drainage ditches throughout the monitoring period. *Carex aquatilis*, a very rare species on the national level, but quite common in our region, showed a decline in the first 5 years, but after 8 years new individuals established in plots that were severely affected by the drainage ditch (Table 2).

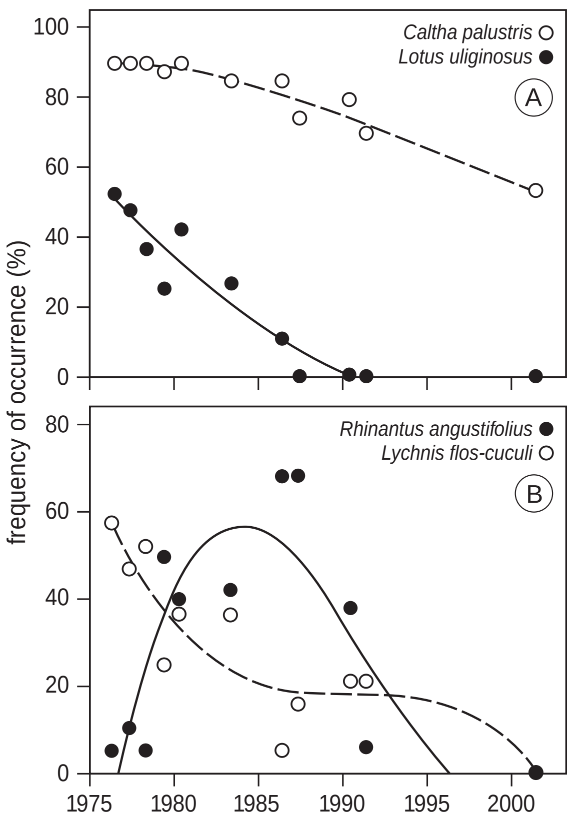

Figure 2. Change in frequency of species over a period of 26 years, measured in 19 permanent plots situated in a hay meadow under the influence of drainage.

Changes in species cover

The mean cover of *C. palustris* showed a distinct increase during the first 5 years, but declined steeply during the second half of the observation period (Fig. 3). The initial increase was most pronounced in plots that were least affected by drainage and was associated with more precipitation in this period (1978–1980). The mean cover of *L. flos-cuculi* showed a steep decrease, which started immediately after the lowering of the water table. *L. flos-cuculi* declined more rapidly than *M. palustris*. The annual *R. angustifolius* and some perennials such as *Holcus lanatus* and *Filipendula ulmaria* showed a significant temporary increase during that period. A slight recovery in 2001 was observed for several species in some wet plots, but perennial grass species such as *Festuca rubra* and *Poa trivialis* gained dominance in most plots at the end of the monitoring period.

Similarity with a local reference type

The time period after which plots reached the 20% similarity with the local reference type depended on the intensity of drainage (Table 3). The most affected plots lost membership of the local reference after 4–10 years, while less affected plots lost membership after 11–20 years. All analysed plots showed a negative trend in similarity with a local reference type.

Table 1. Change in frequency (%) of species occurring in 19 permanent plots situated in a hay meadow under the influence of drainage

	1976	1977	1978	1980	1983	1986	1987	1990	1991	2001
Festuca pratensis	100	89	100	89	95	95	95	37	79	42
Anthoxanthum odoratum	84	89	89	74	79	79	84	68	58	79
Cynosurus cristatus	68	58	63	53	79	32	37	16	5	
Trifolium repens	53	63	53	58	53	53	32	11	5	
Carex aquatilis	32	21	11	16	26	21	16	21	21	37
Potentilla anserina	26	21	21	21	16		5	5		
Carex rostrata	21	5	26	11	5			5		
Eleocharis palustris	16	5	11	11	5	5	5			
Luzula campestris	16	5	5	11						
Dactylorhiza majalis	11	5	11	5	11	5	5	5	5	5
Ranunculus lingua	11	5	5							
Glyceria maxima	11									

Species in bold are Red List species (Van der Meijden et al., 2000).

Table 2. Change in percentage cover of species in three permanent plots close to the drainage ditch

	1976	1977	1978	1979	1980	1983	1986	1987	1990	1991	2001
Carex aquatilis						0.7	0.3	0.3	0.3	0.3	1.3
Caltha palustris	13.3	2.3	3.3	16.7	13.3	2.0	2.0	2.7	0.7	1.0	
Rhinanthus angustifolius				0.3	0.7	0.7	13.3	11.0	0.3		
Festuca rubra	6.0	8.7	7.7	4.0	10.7	10.3	14.0	20.0	40.0	30.0	20.0
Holcus lanatus	8.0	46.7	30.0	13.3	11.3	30.0	1.3	2.3	2.3	1.0	16.7
Species-richness	28.0	21.0	19.0	22.0	27.0	21.0	24.0	20.0	15.0	15.0	19.0
Percentage annuals	0.6			2.3	3.7	4.3	9.7	9.0	1.0		

Note the dramatic decline of the wet meadow species *Caltha palustris* and the increase of the tall sedge *Carex aquatilis*, a species of very wet habitats.

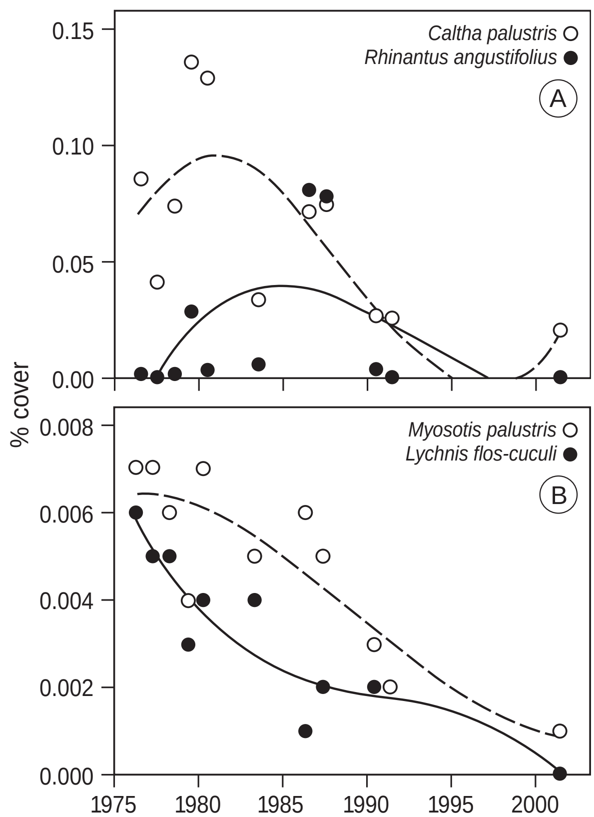

Figure 3. Change in percentage cover of species over a period of 26 years, measured in 19 permanent plots situated in a hay meadow under the influence of drainage.

Table 3. Calculated linear regression between water levels measured in May 1977 and change in similarity with a local reference type measured in 14 permanent plots between 1976 and 2002

Plot no.	Water levels in cm	Linear regression: $y =$	Time to reach 20% similarity in years	R^2
15	20	1.31x–2546.91	20	0.37
19	20	1.43x–2781.21	16	0.45
27	25	1.96x–3833.54	15	0.51
28	26	1.34x–2609.72	14	0.27
23	30	1.34x–2612.92	18	0.33
3	30	1.11x–2136.83	13	0.42
7	45	1.42x–2748.31	11	0.59
20	48	1.75x–3425.22	14	0.50
14	60	1.36x–2643.79	10	0.54
11	60	1.61x–3132.68	9	0.55
13	60	1.41x–2729.29	9	0.45
6	60	1.22x–2354.65	6	0.31
12	70	1.39x–2694.21	9	0.56
10	80	1.15x–2216.11	4	0.25

The time to reach 20% similarity has been obtained from the regression analysis. Only significant relationships are presented.

Reduction of the number of species in the meadow as a whole

In 1976 we found 69 vascular plants in the permanent plots, and 82 in the meadow as a whole, including the surrounding stream and ditches. In 2003 we found 38 species in the permanent plots, and 72 in the meadow as a whole. After 26 years the overall loss of species in the meadow as a whole (including all ditches) was 12%, while the species loss in the permanent plots was 45%.

Discussion

Response to drainage: community level

The speed at which the plots reached a similarity of less than 20% with the local reference type was dependent on the intensity of drainage. Drainage promotes the development of new vegetation types with a dense sward of grasses, from which characteristic species of wet meadows dissappear at different rates. *L. flos-cuculi* showed a much faster decline than *C. palustris*, both in frequency and cover. This species has a high population turnover in which successful establishment of seedlings requires the occurrence of gaps (Biere, 1991). *C. palustris* can survive unfavourable conditions for at least 14 years as an adult, but rejuvenation of the population apparently came to a halt in 1980 when young seedlings of *C. palustris* were registered for the last time (Grootjans & Schipper, 1987). Population dynamic processes are, therefore, likely to be responsible for the different behaviour of characteristic species of the community.

Succow (1986), who studied the long-term effects of deep drainage on fen meadows in eastern Germany, also showed that changes in land use led to new combinations of species (syntaxa). In our case, the vegetation, where *C. aquatilis* invaded a *F. rubra* sward can be seen as another example of a new community that does not easily fit in any existing list of plant communities in the region. The *F. rubra* vegetation is typical of drained peat soils, while *C. aquatilis* is typical of very wet soils (Schaminée, Stortelder, & Weeda, 1996). An explanation of this phenomenon could be as follows: Originally, the surface water flow in the old ditches was directed to the stream (Fig. 4a). After the construction of the drainage channel the ditches in the centre of the meadows received less groundwater and *C. aquatilis* retreated to lower parts of the ditches and to the isolated stream next to the

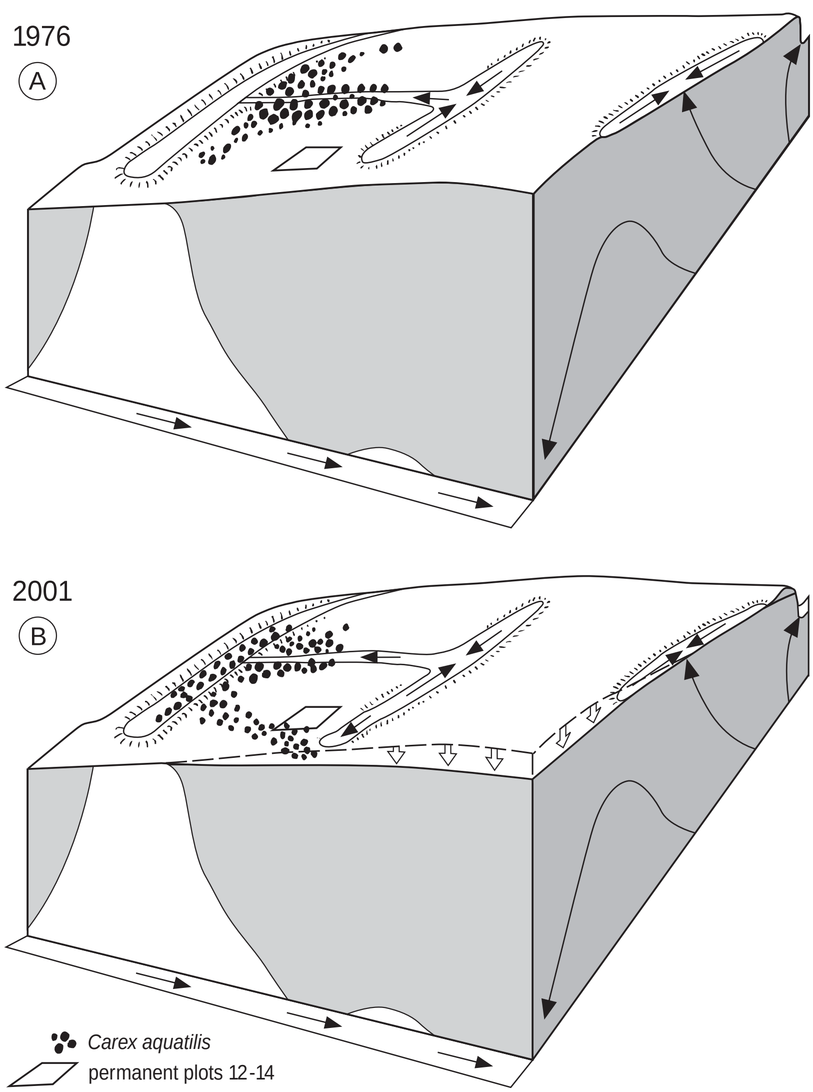

Figure 4. Change in distribution pattern of *C. aquatilis* between 1976 and 2001 in the drained meadow. Through vegetative spread, this tall sedge first retreated in the low-laying parts of the meadow, expanded in the former stream and spread towards an area very close to the drainage channel. That area received ditch water from an old ditch that had changed its flow pattern due to severe peat compaction near the drainage channel.

meadow. Parts of the meadow close to the drainage channel lost almost all "wet" species. During the first 5 years of drainage the N-mineralisation was very intense (Grootjans, Schipper, &Van der Windt, 1985) and grasses, such as *H. lanatus* expanded vigorously. During the last 10 years *F. rubra* became the dominant species, but its cover declined due to wetter conditions. This "rewetting" was caused by a compaction, mineralisation and oxydation of the peat, leading to a lowered surface of the peat. This natural phenomenon occurs after intensive drying of peat soils (Schmidt, 1994). After 25 years of soil compaction, the soil surface near the drainage channel had dropped so much that the direction of water flow of the original ditches had changed (Fig. 4b). In times of heavy rainfall, the water in some ditches now flows to the deep drainage ditch and infiltrates into the peat. *C. aquatilis*, which is a relatively deep rooting species, responds by vegetative expansion into the species-poor *F. rubra* sward, where direct competitors, such as other sedge species or deep-rooting herbs of wet habitats are no longer present. *C. aquatilis* is very close to the most southern limit of its distribution in NW-Europe and very rare in The Netherlands, and in the neighbouring North-German lowlands. Yet, it responds to drainage in a very flexible way, escaping extinction by vegetative growth from still existing populations nearby and exploring new habitats wherever it can find them.

Response to drainage; species level

We found that species with a low initial frequency in the meadow were the first to disappear from the observation plots. These species were found in 1976 along the ditches. They included both rare (*V. dioica*) and common species *Glyceria maxima*, *Sonchus arvense* and *Sparganium erectum*. These changes are clearly related to changes in biotic and abiotic conditions. Local rarity (low initial frequency) as such is, however, not a good predictor for population decline, since *Rhinantus angustifolius* and *Bromus mollis*, which also had a low initial frequency, showed a marked increase in frequency after 5 years, and after that dissapeared again. *D. majalis*, a characteristic species of the *C. palustris* alliance and a rare orchid species maintained a very stable population along the small ditches throughout the observation period. Practically, all characteristic species of the *C. palustris* alliance disappeared from the plots after 26 years. Only *C. palustris* retreated to the wettest plots and remained present with a low frequency. Most of these changes were according to our expectations. What we did not expect, however, is that some common legume and grass species with a high initial frequency (*Trifolium repen*, *T. pratensis*, *C. cristatus* and *Agrostis stolonifera*) disappeared from all the plots. Such species are not known for their sensitivity to drainage and would normally remain when the soil conditions remain moist. Apparently the drainage of (part of) the meadow also triggered some changes in management (less frequent mowing, unfrequent grazing), which could have had an impact on the survival of species.

The overall loss of species richness after 26 years in the plots was approximately 45%. In the whole field, including ditches and surrounding water courses, the decline in species richness was much less (about 12%). The loss in species richness in the observed plots is quite high, considering that at least one-third of the plots only experienced a very minor water table draw-down (less than 10 cm; Grootjans et al., 1996). Apparently, the changes in water regime were associated with long-term changes in management or soil physico-chemical conditions in all the plots, not only the ones that experienced a severe draw-down of 40–80 cm (Grootjans et al., 1985). The drastic decline of relatively eutrophic species, such as *Festuca pratensis*, *A. stolonifera*, *Trifolium* species and *Bellis perennis* indeed point to a decrease in nutrient availability since 1976. All of these species were still present within 50 m around the research area. Species that could not be found again in the meadow or the surrounding area, were amongst others *Triglochin palustris*, *Carex panicea* and *V. dioica*.

So few species really became extinct, but the population sizes of many species drastically decreased and so did their distribution within the field. This decline in polulation sizes may have consequences on population fitness.

Population level

The literature on small populations in landscapes with a changing land use is rather pessimistic on the survival abilities of small populations. Boerrigter (1995), who reported on the regionally rare species *Phyteuma nigrum*, for instance, found a 11% decline of the geographical distribution in the catchment of the Drentse Aa between 1973 and 1991. Several of the remaining populations were reduced by, on average, 64% in local cover. Ecological factors, such as changes in the regional hydrology, may have caused the demographic decline, but genetic factors also may have played a role in addition (Morgan, 1999; Kéry, Matthies, & Spillmann, 2000; Luijten, Dierick, Oostermeijer, Raijmann, & Den Nijs, 2000). Population size is, however, not in itself an adequate indicator of lower fitness. Van Andel, Wesselingh, and Van Donk (1988) tested the vitality of progeny from individual mother plants of *P. nigrum* from a non-declining large population and a declining small population. They did not find differences in the average fitness (measured as dry weight production of the seedlings), but rather in the within-population variability (progeny from the declining population being less variable). For *Gentiana pneumonanthe*, on the contrary, Oostermeijer, Van Eijck, and Den Nijs (1994) concluded from a comparison between offspring from 19 differently sized populations, that progeny from small populations showed a reduced fitness, indeed, but that the seedlings may be phenotypically more variable at the same time.

These examples indicate that in addition to environmental threats, such as drainage, genetic processes can enhance the decline of small populations, but also that the literature on this subject is far from conclusive. It is, however, also clear that information on changes in geographical distribution often underestimates the rate of decline, which implies that the population fitness should be taken into account (Oostermeijer, Luijten, & Den Nijs, 2003). For monitoring purposes, population sizes are useful indicators, in addition to the geographical distribution of a species, even when there is no consensus about the underlying mechanisms of polulation decline.

The problem of scale

Like the local plots, the whole meadow shows a decline in species richness. However, the rate of decline seems to be significantly lower than the decline on the local scale. About 12% of the species have disappeared from the meadow, creating a much more optimistic image of the state of the meadow species richness than the local-scale survey, which showed a 45% drop in species richness. Furthermore, observations on the scale of the whole meadow do not reveal the dynamics within the meadow (such as the formation of transient community types). They do, however, provide information about population sizes, and function as a frame of reference for local observations. Therefore, it is preferable to use different-scaled approaches in ecological evaluation procedures.

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