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30 years of hay meadow succession without fertilization: how does it affect soil and avifauna groups?

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Zusammenfassung: Die vorliegende Studie thematisiert am Beispiel der Fließgewässerniederung der Drentse A, einem großflächigen Schutzgebiet im Nordosten der Niederlande, die Folgen einer langjährigen Heuwiesennutzung ohne Düngung. Im Einzelnen wurde von uns die Zusammensetzung der Vegetation und Bodenfauna auf fünf Grünlandflächen untersucht, die sich in der Dauer der Ausmagerung unterschieden. Getrennt betrachtet wurden dabei die bachnahen, moorigen Niederungsbereichen und die angrenzenden sandigen Geestbereiche. Die ausgewählten Grünlandflächen waren zum Zeitpunkt der Aufnahmen seit 5, 15, 25, und 32 Jahren gemäht aber nicht mehr gedüngt worden. Eine weitere, nach wie vor konventionell bewirtschaftete Wiesenfläche (incl. Düngung) diente als Kontrolle. Auf allen Flächen wurde die Vegetation und Regenwurmfauna in 10 Plots mit einer Größe von jeweils 4 m² bzw. 0.04 m² untersucht. Darüber hinaus wurden über 28 Jahre hinweg die Brutvögel des Gebietes mittels Revierkartierung erfasst.

Die Pflanzenartendiversität hat sich mit Dauer der Ausmagerung signifikant erhöht. Sie stieg in den bachnahen Bereichen von 13 Arten in der Kontrollfläche (40 m²) auf 49 Arten in der am längsten ausgemagerten Grünlandfläche an. In den trockenen Geestbereichen war der Anstieg deutlich schwächer. Bezogen auf die Gesamtfläche von 40 m² wurden die meisten Arten hier in der 15 Jahre lang ausgemagerten Grünlandfläche gefunden, während bei Betrachtung der 4 m² großen Aufnahmepunkte die höchste Artenzahl ebenfalls in der ältesten Untersuchungsfläche lag. Die Diversität und Abundanz der Regenwürmer nahm mit Dauer der Ausmagerung ab. Die festgestellten Arten gehörten zu 4 Gattungen, wobei die Gattung *Allolobophora* am individuenreichsten vertreten war. Mit Dauer der Ausmagerung sank besonders im trockenen bachfernen Geestbereich der Boden-pH-Wert auf unter 3,8 ab. Die damit einhergehenden pessimalen Lebensbedingungen erklären hinreichend die geringe Diversität und Dichte von Regenwürmern in diesen Bereichen. An fast allen Standorten sank die Biomasse der Regenwürmer zum Sommer hin auf Werte unter 25 g/m², so dass für viele Limikolen zu dieser Zeit pessimale Ernährungsbedingungen bestehen.

Die Zahl der Brutvogelarten war aufgrund des recht kleinen Untersuchungsgebietes insgesamt gering. Dennoch konnten auffallende Veränderungen in der Brutvogelgemeinschaft beobachtet werden. Während Limikolen wie Kiebitz (*Vanellus vanellus*) und Uferschnepfe (*Limosa limosa*) vollständig aus dem Gebiet verschwanden, wanderten der Große Brachvogel und die Bekassine ein. Allerdings sind auch sie aktuell nur noch selten im Gebiet vertreten. Dafür hat sich inzwischen das Schwarzkehlchen (*Saxicola torquata*) als Brutvogel eingestellt – möglicherweise eine Folge der sich ändernden Grünlandvegetation (hier: Zunahme von Pflanzenarten, die als Ansitzwarten fungieren können wie etwa *Cirsium palustre*) in Kombination mit einem verbesserten Nahrungsangebot an Makroinvertebraten. Eingewandert sind zwischenzeitlich auch eine Reihe weiterer Vogelarten, wie Pirol (*Oriolus oriolus*) und Kleinspecht (*Dendrocopos minor*), die charakteristisch für sich entwickelnde Bruchwälder sind. Letztere haben sich, meist kleinflächig, auf ehemaligen Feuchtgrünlandstandorten entwickelt.

Summary: In the present study we investigated the effects of hay meadow succession in the brook valley system of the Drentse A Nature Reserve, in the NE of the Netherlands. In particular, we compared the plant and soil fauna composition in five grasslands that differed in the stage of vegetation succession in two well-studied chronosequences, dry and wet respectively.

The sampled meadows include a control site (still fertilized meadow), a 5, 15, 25 and 32 years stage of vegetation succession after the cessation of fertilizer application. At all sites, vegetation and earthworm composition was studied in replicate subplots of 4 m² respectively 0.04 m² each. Moreover, the breeding birds have been monitored in the area over the last 28 years by mapping territories overlapping the meadows of the chronosequences.

Concerning the plants we found that diversity was increasing with time of succession. In the wet meadow series the plant species richness increased from ca. 13 species per site (40 m²) to a maximum of ca. 49 species per site in the latest successional stage. In the drier parts the increase in species was less and reached an over all maximum of 27 species in the intermediate (15 years old) stage of the succession in 40 m², but still increased to a mean of 15 species at the scale of 4 m² plots in the oldest stage. The diversity and abundance of earthworms dropped significantly over time of succession. The species all belonged to 4 genera with *Allolobophora* being the most abundant. Soil pH dropped significantly during the succession even below 3.8 in the dry series. This largely explains the unfavourable conditions for the earthworms to survive in the oldest stages of the dry succession. The earthworm biomass dropped in nearly all sites below 25 g/m² during the summer period, indicating unfavourable conditions for a suit of grassland breeding waders.

The abundance of breeding birds in general was low due to the rather small area covered in this study. Anyhow we could find obvious changes in the breeding bird community. In particular waders such as Lapwing (*Vanellus vanellus*) and Black-tailed Godwit (*Limosa limosa*) disappeared completely from the area and were followed up by Curlew (*Numenius arquata*) and Snipe (*Gallinago gallinago*) being currently also rare in the area. Probably due to changes in grassland vegetation (increase of amongst others *Cirsium palustre*) and insect abundance the Stonechat (*Saxicola torquata*) has entered the area as a breeding bird. The same happens to a set of bird species typical for developing carr woodlands such as Lesser Spotted Woodpecker (*Dendrocopos minor*) and Golden Oriole (*Oriolus oriolus*).

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1 Introduction

Species rich wet hay meadows are a threatened type of semi-natural grassland in Europe which receives special attention in several countries including The Netherlands. These meadows are special for their set of plant species belonging to the prevailing specific abiotic conditions such as high ground water levels, peaty and sandy soils and local feeding with calcareous seepage water along brooks. Nature management in the meadows generally is focused on the removal of biomass and accompanying nutrients by yearly hay making (Bakker 1989). Much knowledge is available on the processes that govern the conservation and restoration of these wetlands (Wheeler et al. 1995, Bakker & Berendse 1999, van Andel & Grootjans 2006). However most of this information comprises the ecohydrological and landscape ecological features that concern the plant compartment of this system. Most of these processes take place on a time scale of decades or more. Not much is known about how the plant-focused management affects the soil fauna and avifauna in these meadows over longer time periods.

A hot item in the European policy for nature conservation concerns the protection of meadow birds. Much research has been carried out to assess the processes and mechanisms responsible for the decline in numbers of breeding pairs of so-called critical meadow birds or grassland breeding waders in Northwest Europe such as loss of suitable breeding habitats, predation, tree encroachment (Beintema 2005, Teunissen et al. 2005b, Valkama et al. 1999, Berg et al. 1992, Baines 1990). The ongoing debate often discusses the choice that conservation managers and land owners should make between aiming either high plant species diversity or high densities of grassland breeding waders at their sites as both aims do not seem to be able to unite (Dijkstra 1991, Bakker & Olff 1992, Beintema & Müskens 1987, Van Wieren & Bakker 1998 in Grazing and Conservation Management).

This study evaluates the effects of long-term management aimed for the restoration of plant diversity on the development of the bird populations over a period of 30 years in a well-studied chronosequence along a brook valley in the Netherlands. To provide a solid link between the two compartments of the ecosystem, plants and grassland-breeding waders, we also gathered data on one important food source of the birds, the earthworm population in the soil beneath the vegetation under succession. Additionally, we investigated a set of habitat parameters such as soil properties of the sites to explain the successional changes in terms of habitat changes for the soil macro-fauna.

2 Study area and sampling methods

2.1 Study area

The study area is situated at the Drentsche A Nature Reserve, The Netherlands (53°N, 6°42'E). A set of fields along the Anloërdiepje brook valley have been acquired by the State Forestry Commission individually over a period of 30 years. These sites differ in their so-called 'age of succession' and therfore in plant species composition and soil fertility due to the different years at which fertilizer application ceased and the original hay-making regime (cut once a year at mid July) was resumed (Bakker 1989, Bakker & Olff 1995). In one of these fields monitoring of the vegetation took place from the very beginning of the cessation of fertilizer application and represents a full time series, the other fields are dated from their years of restoration management and they each represent a physical stage of the succession. The present set of fields with different years of cessation of fertilizer application forms a chronosequence representing a successional series of soil impoverishment in a wet and a dry grassland habitat. (Bakker & Olff 1995). The dry sequence on sandy soil, situated on the higher elevated sandy edges of the brook valley, consisted of five fields managed for 1 (control), 5, 15, 25 or 32 years (see Fig. 1). The wet sequence is situated on peaty soil adjacent to the brook in fields with the same age history as the dry series. None of the fields were grazed. In both series the control field was the most nutrient rich as fertilization had only stopped the year before.

The vegetation development at the 25 year old dry and wet site has been studied from the start of the cessation of fertilizer application up till now by Bakker & Olff (1995) and comparison of the data from permanent plots at this site was used to confirm the successional age of the other sites and thus validate the chronosequence.

Within the dry series the vegetation ranges from a *Holcus lanatus* dominated community to an *Agrostis capillaris-Luzula campestris* community. The wet series ranged from a *Poö-Lolietum* to a *Juncus acutiflorus* dominated community (nomenclature of plant species follows Van der Meijden, 005), both representing retrograde successions in response to impoverishment. Soil fertility has now been restored to values typical of the hayfields at the beginning of this century before the application of both artificial fertilizer and large amounts of cattle manure had started. However, the plant species composition in each series has not yet returned to that of the target communities and is still changing due to the fragmentation of the landscape around the reserve. Some plant species have become locally extinct during the past 50 years and therefore the actual succession is now mainly being constraint by dispersal limitations of plant species (Bekker et al. 1998).

2.2 Sampling

The plant species composition was recorded in the summer of 1999 in each of the five sites of the dry and wet chronosequences that differ in age since last fertilization (1, 5, 15, 25 and 32 years). At each of the fields 10 plots of 2m x 2m where laid out where all plants and their abundances were recorded.

The soil macro fauna (*Lumbricidae*) was sampled in spring, summer and autumn of 1999 in 24 samples of 0.4 m^2 to a depth of ca. 20 cm at each of the five stages in both the dry and the wet chronosequence. We collected the earthworms by hand sorting and fixated them in ethyl alcohol (80%). After species identification the individuals were weighed to calculate the fresh biomass. Biomass and diversity of earthworms were summed into a full season dataset. In each sample soil pH was measured, using pH 0.01 M $CaCl_2$, and soil moisture content was determined.

The fields in the chronosequence contain a large number of permanent plots which have been recorded each year since 1976 during the same time period each year. Nearly always this was done by the same person that as a side-interest, also recorded the grassland and woodland breeding birds territories in the study area. However, the mapping of the birds' territories was restricted to meadowbirds and species vulnerable on a national scale. Thus common breeding birds, e.g. Chaffinch (*Fringilla coelebs)* and Great Tit (*Parus major*), were not recorded. This unique dataset was modified for our purposes to track changes in the meadowbird community in this brook valley: As the fields under study are very small we decided to subdivide the whole brook valley into two subplots 1 and 2 (see Fig. 1). Both blocks have a size of 13 hectares, of which only the meadows have been included in the counting. This results in ca. 7 hectares of study area in each of the blocks. To provide for matching with the successional stage of the study sites the period of recording was also subdivided into two time intervals: 1976-1990 and 1991-2004, where the combination of plot one and the first time period represents the control till a mean of five years of restoration management. Plot one

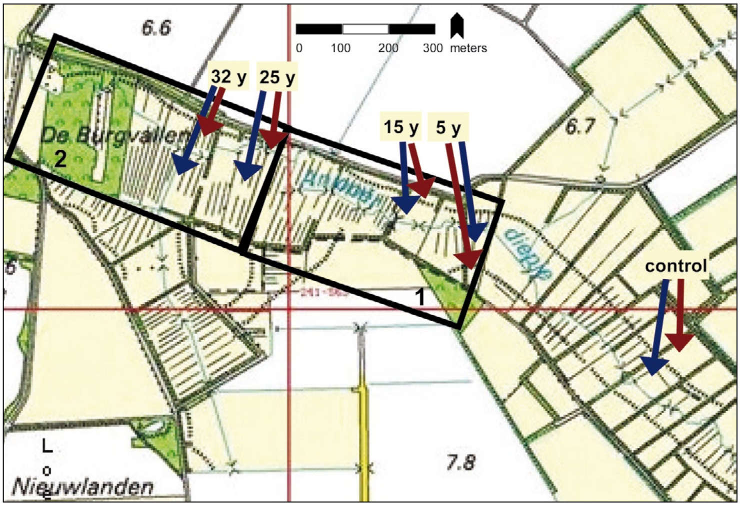

Fig. 1: Study area Anloërdiepje (The Netherlands) with sites indicated with age of succession, red arrows indicate the dry locations; the wet sites are marked with blue arrows. The two plots for monitoring of bird territories are marked in black and numbered 1 and 2 respectively.

during 1991-2004 represents the sites with a mean of 15 years of restoration management. Plot two in combination with the two periods represents the means of 20 and 30 years of haymaking without fertilizer application respectively. We summed up all the birds territories over the periods per subplot per bird species and also made no distinction between the dry and the wet series. In our analysis we separated between grassland breeding waders and indicative woodland birds. As there is no sharp definition of meadow birds we followed Beintema and coworkers (1995) who defined several meadow birds via their habitat preferences. In particular, they classified 28 species as meadow birds from which 14 depend on managed grassland for a larger part of the population, the grassland breeding waders that we will focus on in this study.

2.3 Data analysis

Changes in the plant species richness and the biodiversity of earthworms over the successional period were analysed separately for the dry and the wet series. In particular, we used One-way-ANOVAs from the software package SPSS 12.0 to check for significant differences in the mean number of plant species per vegetation plot and the mean number of earthworm species per soil sample respectively. In case of significance the variance analyses were followed by Scheffe post-hoc-tests to locate the significant differences.

Changes in the biomass of earthworms in soil samples taken in spring, summer, and autumn from grasslands which differed in the period of non-fertilization were checked by Two-way-ANOVA. One factor represented the period since cessation of fertilizer application (5 levels: 5, 15, 25, 32 years of restoration management and a control field), and the other the time of the year (3 levels: spring, summer and autumn). A priori a Levene's test for homogeneity was performed and after the ANOVA a post-hoc test waqs used to indicate significant differences between the groups.

The changes in numbers of birds territories have been analysed by a One-way-ANOVA where the defined blocks x time period represented the successional stages. Also here a priori a Levene's test and a posteriori a post-hoc test were performed to indicate significant differences between groups.

Moreover the community composition of the breeding birds has been analysed with a DetrendedI Correspondence Analysis with the software package PC-Ord 4.25, where the factor Time since last fertilizer application was used to define the separation of the species along the DCA axis 1 and 2.

3 Results

3.1 Changes in plant species composition

The plant species richness increases significantly over the successional period in both the dry and the wet chronosequences. The dry series had a maximum of 27 species per 40 m^2 reached already in the intermediate stage of 15 years without fertilization application. While no significant changes in plant species richness were found in the older stages of the dry series at the site level, still an increase in species was found on the local plots level. However, with respect to the wet series we revealed a constant increase in the number of plant species with time of soil impoverishment at both the plot and the site level. Thus the wet series reached a maximum of 49 species per 40 m² at the oldest site under restoration management (Fig. 2 and Fig. 3).

The vegetation in the dry series was dominated by a few small grasses (*Festuca rubra agg.* and *Agrostis canina*) and contained a high percentage of mosses (most *Rhytidiadelphus squarrosus*) in the late successional stages. The biomass decrease in these sites ranges from 6 to 2 ton/ha. In the wet series *Juncus acutiflorus* dominated the vegetation accompanied by *Anthoxanthum odoratum, Dactylorhiza majalis, Viola palustris* and *Sphagnum* spp. as indicator species of the later stages. The canopy height had increased on average only in the wet series but the biomass production from these sites decreased from 8 ton/ha to 4.5 ton/ha.

3.2 Changes in the earthworm communities

During the course of the succession the diversity of earthworm species drops significantly in both the dry and the wet series. Overall, a striking low number of species is found in both series, with a maximum of 2.45 species per 0.04m² at the intermediate stage of the wet successional series. In general the wet series is slightly more diverse (Fig. 4).

The mean number of individuals of four species groups of earthworms over the two successional series shows a strong decline overall species groups (Table 1). Only two groups of species had enough data for a statistical test, but both groups show a significant decline over time with the lowest abundance in the oldest, 32-year-old stage of succession in both series. The dominant species in both series was *Aporrectodea caliginosa.*

The biomass of the earthworms varied significantly during the season of the year and between sites with different successional age in both series (Table 2). Overall the summed biomass of the whole season was higher in the wet series than in the dry series, varying from slightly higher to a 2-10 fold difference per stage. The maximum of the annual mean biomass per site was 187 g/m², reached in the control site of the wet series.

3.3 Soil parameters during succession

The pH values of the sites varied between 3.45 and 6.35 in both series. We did not find a correlation between earthworm biomass and pH in the dry series but we did find one in the wet series (Pearson correlation: $r = 0.31$, $p = 0.001$) although not very strong. In the wet series the pH in hardly any of the soil samples comes below the threshold value of pH 3.8 (Fig. 5). At this value toxic metals such as Al start to dissolve which drastically reduces the suitability of the habitat

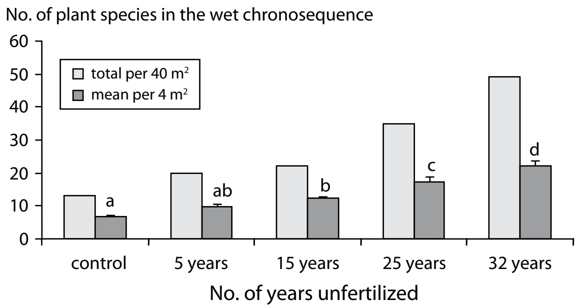

Fig. 2: Total and mean number (+ s.e.) of plant species in each stage of the wet successional series. Different letters refer to statistical differences (p<0.05) obtained for each series by a Scheffe-post-hoc test, after a One-way-ANOVA, p<0.05.

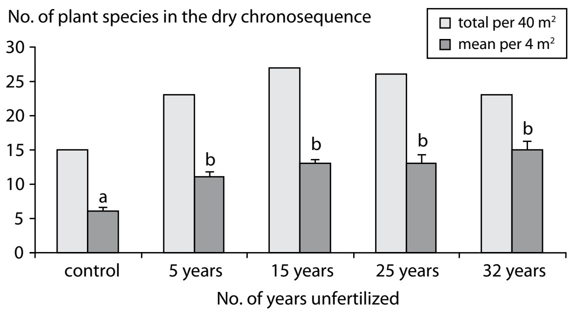

Fig. 3: Total and mean number (+ s.e.) of plant species in each stage of the dry successional series. Different letters refer to statistical differences (p<0.05) obtained for each series by a Scheffe-post-hoc test, after a One-way-ANOVA, p<0.05.

Table 1: Changes in the number of individuals of different earthworm worm groups in soil samples taken from meadows on sandy soils (Dry series) and from peat soil (Wet series) which have not been fertilized since 5, 15, 25, 32 years and a control field. Different symbols indicate significant differences ($p < 0.05$) assessed by One-way ANOVA which in case of significance was followed by a Scheffe-post-hoc-test.

Species	Series	Control	5 yr	15 yr	25 yr	32 yr
A. species	Dry	$2.25 \pm 0.5^{a,b}$	3.39 ± 0.61^{a}	$0.88 \pm 0.28^{b,c}$	$1.78 \pm 0.5^{a,b,c}$	0.04 ± 0.04^{c}
	Wet	5.33 ± 1.3^{x}	6.63 ± 1.15^{x}	5.10 ± 1.00^{x}	$2.4 \pm 0.9^{x,y}$	0.5 ± 0.27^{y}
D. species	Dry	0 ± 0	0 ± 0	0.18 ± 0.18	0 ± 0	0 ± 0
	Wet	0.07 ± 0.07	0 ± 0	0.10 ± 0.07	0.30 ± 0.25	0.26 ± 0.17
L. species	Dry	$0.95 \pm 0.4^{a,b}$	$0.33 \pm 0.14^{a,b}$	$0.59 \pm 0.33^{a,b}$	1.28 ± 0.34a	0.09 ± 0.06^{b}
	Wet	0.73 ± 0.23	0.53 ± 0.28	1.80 ± 0.30	1.15 ± 0.33	0.53 ± 0.30
O. species	Dry	0.05 ± 0.05	0.28 ± 0.28	0 ± 0	0.17 ± 0.12	0 ± 0
	Wet	0.40 ± 0.21	1.52 ± 0.38	1.60 ± 0.60	0.80 ± 0.32	1.00 ± 0.34

A. species comprised: *Aporrectodea caliginosa*, *A. chlorotica* and *A. rosea*. D. species contain only *Dendrodrilus rubidus*. L. species consisted of *Lumbricus castaneus* and *L. rubellus*. O. species represented *Octolasion cyaneum* and *O. tyrtateum*.

Table 2: Mean biomass (g/m^2) of earthworms in soil samples taken in spring, summer and autumn from meadows on sandy soils (Dry series) and from peat soil (Wet series) which have not been fertilized since 5, 15, 25, 32 years and a control field. Statistics obtained by a Two-way ANOVA with season and successional age as effects. Samples with the shells of molluscs are excluded from the analyses.

		Control	5 years	15 years	25 years	32 years
Dry series	Spring	32.19	35.86	39.06	37.32	0.50
	Summer	6.18	10.64	1.77	17.04	1.21
	Autumn	22.07	39.45	73.47	28.16	3.67
Total season mean		60.44	85.95	114.30	82.52	5.38
Wet series	Spring	73.45	70.94	68.99	42.28	16.91
	Summer	18.93	18.33	41.09	23.98	30.24
	Autumn	94.76	38.97	33.29	21.58	14.97
Total season mean		187.14	148.24	143.37	87.84	62.12

Statistics:

Dry series	**df**	**F**	**Sig.**	**observed power for alpha = 0.05**	
Season effect	2	6.905	0.002	0.913	**
Successional age effect	4	12.950	0.000	1.000	***
Season x successional age	8	2.1 68	0.040	0.817	*
Wet series	**df**	**F**	**Sig.**	**observed power for alpha = 0.05**	
Season effect	2	12.670	0.000	0.996	***
Successional age effect	4	7.519	0.000	0.992	***
Season x successional age	8	5.822	0.000	0.999	***

for earthworms. Quite a few of the samples in the dry series fall in the toxic Al-buffer range of the substrate, especially those in the oldest dry site (32 years not fertilized). Here pH was that low (3.5 -4.2) that very low biomass of worms was detected, if at all. The measurements on soil moisture content proved the large difference between the two series and also that soil moisture content varied over the sites (data not shown). Especially the oldest stages within the wet series were found to have much higher soil moisture content, especially in spring. This effect almost failed to appear later in the year.

3.4 Changes in the breeding bird community

The mean number of grassland breeding waders and indicative woodland bird species declined significantly from 3.8 to 2.3 over all successional stages during the last 30 years (Fig. 6). In the first 10 - 15 years of the recording period a total of 26 to 32 breeding pairs were observed. Thereafter the number dropped to 18 in the latest successional stage. The same trend was observed when we only count the number of grassland breeding waders in the area. These numbers vary around 15 during the first 25 years of succession, however, in the latest stage of succession just up to five pairs have been observed.

A strong shift in the species composition of the birds has taken place with the years of succession (Fig. 7). The DCA axis 1 and 2 explain 69% and 5% of the variation respectively. Particular waders such as Lapwing (*Vanellus vanellus*) and Black-

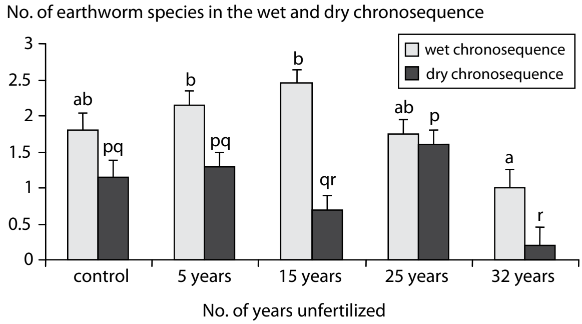

Fig. 4: Mean number of earthworm species (+ s.e.) in the dry and wet successional series. Different letters refer to statistical differences ($p<0.05$) obtained for each series by a Scheffe-post-hoc test, after a One-way-ANOVA, $p<0.01$.

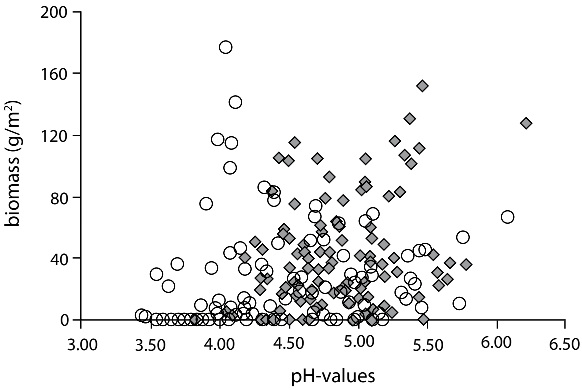

Fig. 5: The pH values in each of the earthworm biomass samples in the dry (open black circles) and the wet successional series (closed grey diamonds).

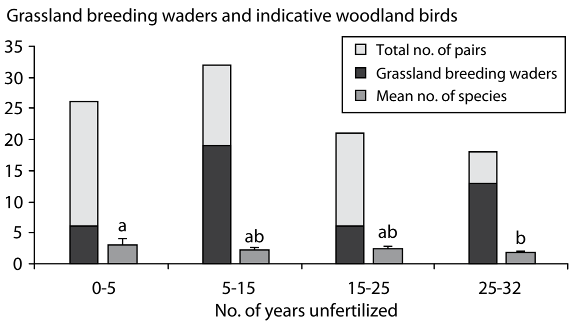

Fig. 6: The number of breeding pairs of all birds, and the number of grassland breeding wader pairs in four stages of the successional series. The mean number of bird species (+ s.e.) is shown separately. Different letters refer to statistical differences ($p<0.05$) obtained for each stage by a Scheffe-post-hoc test, after a One-way-ANOVA, $p<0.05$.

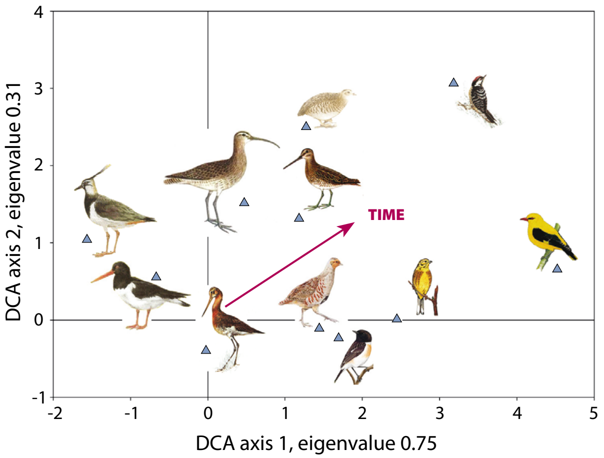

Fig. 7: The first two DCA-axes depicting the change in species composition of the breeding birds in the Anloërdiepje brook valley during 32 years of succession (arrow indicates the factor Time). Species involved in the analyses (from left to right) Lapwing, Oystercatcher, Black-tailed Godwit, Curlew, Snipe, Partridge, Quail, Stonechat, Yellowhammer, Lesser spotted Woodpecker and Golden Oriole.

tailed Godwit (*Limosa limosa*) were present at the start of the succession but decreased and have completely disappeared from the area in later stages. They were followed up by Curlew (*Numenius arquata*) and Snipe (*Gallinago gallinago*) being currently also rare in the area. The Stonechat (Saxicola torquata) has entered the area as a breeding bird. The same happens to a set of bird species typical for (developing) carr woodlands such as Lesser Spotted Woodpecker (*Dendrocopos minor*) and Golden Oriole (*Oriolus oriolus*).

4 Discussion

The number of plant species in both chronosequences still increased, although slowly, over the years after cessation of fertilizer application. Apparently, in the wet series the germination and establishment of incoming species is still possible on the plot scale and the site scale, where in the dry series the ecological factors on the site scale changed in such an unfavourable way (especially pH, contents of bases in the soil but also the extensive moss cover) that additional species of the surrounding areas are not able to establish there anymore, however species richness at the plot level still increased. This is in accordance with the long-term observations of Kapfer (1998) and Bakker (1989), and also points to the fact that the brook valley as a whole seems to dispersal limited.

Although plants species richness on the whole has increased, earthworm richness and biomass have decreased during succession. With regard to the latter it is well known that the soil-pH is an important factor for the occurrence and biomass of earthworms (Düttmann & Emmerling 2001). Just a couple of species are known to be acid-tolerant (Beylich & Graefe 2001). Therefore it is likely that the decline of soil-pH in the drier parts of the brook valley as a result of long-lasting non-fertilization has changed the earthworm community considerably. However, changes in soil-pH cannot explain the decrease in the density and biomass of earthworms with the time of cessation of fertilizer application in the wet part of the brook valley. Two other factors might be responsible for our finding: (1) inundations, especially in winter and early spring, and (2) limitations in macro-nutrients. With regard to the former it is well known that long periods of inundation are able to cause a severe decline in soil-macroinvertebrates via oxygen depletion (Ausden et al. 2001). Indeed, the oldest stages of the wet series were inundated just before we took our first soil samples in spring 1999. Previous research has shown that (in addition to soil type) species composition and location relative to the brook, the wet and the dry series, differed in the type and extent of macro-nutrient limitation (Olff & Pegtel 1994; Pegtel et al. 1996). However, the nature and extent of the reaction of the earthworm species to various limiting macro-nutrients superimposed to the difference in soil moisture content between the two series is until now not very well understood.

The number of bird species in this study was rather low most likely due to the relatively small research area, and stayed rather constant over time. The latter finding is in contrast to expectation and literature results which report an increase in species and breeding numbers with increasing landscape elements, e.g. trees, hedges, and mid-field woods (Puchstein 1980, Bezzel 1982, Kujawa 1997). This difference, however, is almost exclusively due to different bird census techniques, since we exclusively focussed on target species, notably meadowbirds and birds vulnerable on a national scale. Even though our data of bird abundance have not been especially collected for monitoring the changes in breeding bird communities related to hay making succession and changes in landscape structure the unique data set proofs to be suitable to describe a very clear trend in bird species replacement. In particular, the type of target species has changed dramatically from (non-)-critical grassland breeding waders to indicative bird species of (carr) woodlands.

Reduction of available food sources such as earthworm density in combination with a less open landscape may largely explain the decrease in grassland breeding waders in this area. Especially grassland-breeding waders depend to a large extent on soil-macroinvertebrates (Beintema et al. 1991). Biomass of earthworms in conventionally managed dutch farmland often varies between 60 – 300 g / m^2. According to Oosterveld et al. (2004) biomasses lower than 25 g per m^2 are critical in meadowbird areas. Table 2 shows that our study sites maintained a large enough biomass of earthworms in spring but hardly any of the sites under study did exceed this threshold value of critical earthworm biomass during the summer season. This points to a major constraint for the grassland breeding waders.

The conservation management, the hay-making, takes place largely after the hatching of the chicks, so this is not a factor responsible for the decline. The changes in canopy structure however, open but slightly higher, can contribute to the lack of comfort or too short vision for safety for the birds. Where 30 years ago non-fertilized hay-meadows occurred intermingled with fertilized grasslands, nowadays the constant management of nearly the whole brook valley by the State Forestry Commission may have brought a large uniformity in the landscape seen from the meadowbirds perspective. The grassland-breeding waders differ in their habitat preferences. Lapwing chicks forage on meadows with short vegetation, e.g. freshly mown grasslands or grasslands with dairy cattle, while Godwit chicks depend on insects which they pick up from the vegetation. In the past both species benefited from the mosaic landscape management of the grasslands which fails today.

The landscape elements only increased slightly over the 30 years, but most wooded hedge banks became overgrown by a few dominant trees. Recently, the State Forestry Commission has taken on the clearing of quite a few of these wooded hedge banks, which results in a more open and connected landscape. With this practice a number of trees that might have been suitable as perches for birds of prey have been removed since 2004. Predation of clutches and chicks is a growing problem in many meadowbird areas. A few long-term studies indicate that the daily predation risk for clutches of grassland breeding waders has increased in the last decades (Chamberlain & Crick 2003, Teunissen et al. 2005a). With regard to the Netherlands, high levels of predation (higher than the countrywide average) are currently found in the more elevated regions in the north and east (Teunissen et al. 2005b). What are the causal factors for an increasing impact of predators? First, we have evidence that the populations of several predator species of clutches and chicks of meadow birds have increased in the last decades. Due to rabies vaccination and a decline in culling efforts Red Foxes, for instance, increased in density and subsequently colonized new habitats, e.g. open grasslands, rewetted bogs and cities (Bellebaum 2003, Reynolds 2000, Junker et al. in this volume). Additionally, several predators might have benefited from changes in the landscape structure. Many grasslands in elevated regions inside Northern Germany and slightly less in The Netherlands are currently less open than 50 years ago. In these regions many wet grasslands were left fallow or became afforested due to changes in agricultural practice (Strijker 2005). These changes in landscape structure seem to go along with a higher predation risk for ground-breeding birds: Berg and co-workers (1992) demonstrated that the hatching success of Lapwing clutches correlated with the distance to wooded hedge banks and woodlands.

However, despite large scale changes in land use and landscape configuration that took place over the last 30 years in The Netherlands, the present study shows that in a hardly changed nature reserve with a consistent hay making practice aiming for the increase and maintenance of plant diversity, the grassland breeding waders were (almost) lost from the ecosystem and replaced by a different suit of birds. The cessation of fertilizer application in this grassland area has definitely increased plant diversity but minimized the population of grassland breeding waders and one of their main food sources the earthworm population. These findings underline the necessity of the formulation of clear goals for conservation management such that monitoring and evaluation of these goals may lead to the fine-tuning of conservation practices in one area and the avoidance of conflicting goals in other areas.

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