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Do restoration measures rehabilitate fauna diversity in raised bogs? A comparative study on aquatic macroinvertebrates

Gert-Jan A. van Duinen[1,2,*], Ankie M.T. Brock[1], Jan T. Kuper[1], Rob S.E.W. Leuven[2], Theo M.J. Peeters[1], Jan G.M. Roelofs[3], Gerard van der Velde[4], Wilco C.E.P. Verberk[1,4] & Hans Esselink[1,4]

[1]*Bargerveen Foundation,* [2]*Department of Environmental Studies,* [3]*Department of Aquatic Ecology and Environmental Biology and* [4]*Department of Animal Ecology and Ecophysiology, University of Nijmegen, The Netherlands;* [*]*Author for correspondence: Bargerveen Foundation/Department of Environmental Studies, University of Nijmegen, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands, Tel: +31 24 3653275, Fax: +31 24 3653030, E-mail: duinen@sci.kun.nl*

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Abstract

To assess whether raised bog restoration measures contribute to the conservation and restoration of the fauna diversity, macroinvertebrate species assemblages were compared between water bodies created by rewetting measures and water bodies which have not been subject to restoration measures, but are remnants of former peat cuttings and trenches used for buckwheat culture in the past. The restoration sites were inhabited by characteristic raised bog species and rare species, but their numbers were higher at the remnant sites not affected by restoration management. A considerable number of characteristic and rare fauna species were only found at the remnant sites. The remnant sites included considerably more variation in macroinvertebrate species assemblages and had a higher cumulative species richness. The number of characteristic macroinvertebrate species was not clearly related to the presence of a characteristic raised bog vegetation. In restoration sites numbers of rare and characteristic species per site tended to increase with the time elapsed after rewetting. However, restoration measures will not automatically result in restoration of a more or less complete macroinvertebrate species spectrum, as restoration measures have so far resulted in habitats for only a limited number of the characteristic species. When planning restoration measures, it is recommended to protect the populations of rare and characteristic species present in the area, as these populations may become the sources for colonization of rewetted sites. Safeguarding habitat diversity during the restoration process and restoration of different elements of the habitat diversity of complete raised bog systems will result in the characteristic fauna diversity being conserved and restored more successfully.

Introduction

At the moment rewetting measures are taken in many raised bog remnants in western Europe to conserve and restore raised bog flora and fauna. Small- and large-scale drainage, peat cutting and cultivation (e.g. buckwheat culture) have resulted in the degradation and disappearance of raised bog systems (Verhoeven, 1992; Schouten et al., 1998). It can be expected that a number of characteristic fauna species have declined or disappeared as a consequence of the disappearance of the various habitats of pristine raised bog systems. At the same time, however, human activities have also resulted in new habitats within the bog landscape. Dehydration and mineralisation of peat and the inlet of minerotrophic or nutrient-rich water have changed water and soil qualities (Lamers et al., 1998a and 1998b). As a result, species which do not occur under ombrotrophic (i.e., acid, nutrient-poor) conditions were able to establish in bog remnants (Göttlich, 1980; Wheeler and Shaw, 1995; Irmler et al., 1998). For some of these species, the original habitats have been degraded or have disappeared as a result of cultivation, making bog areas nowadays a refugium for species which were originally not dependent on raised bogs (Akkermann, 1982; Schouwenaars et al., 2002). During the last century, flora and fauna species assemblages in raised bog areas have also been affected by increased nutrient availability due to increased nitrogen deposition (Bobbink et al., 1998).

During the last four decades drainage ditches have been blocked and bunds and weirs have been build to rewet drained and cutover raised bog remnants with rainwater. In some cases, these measures have resulted in the recovery of a *Sphagnum* vegetation or the formation of floating rafts on which a characteristic hummock-hollow vegetation establishes, including e.g. *Sphagnum magellanicum, S. papillosum,* and *S. rubellum* (Verhoeven, 1992; Lamers et al., 1999). However, *Betula* sp. and *Molinia caerulea* have invaded most of these sites and large areas of inundated cutover peat still consist of open water with only *Sphagnum cuspidatum* (Schouten et al., 1998).

The aims of nature management generally include the conservation and restoration of a complete species spectrum, paying special attention to characteristic and threatened or Red-Listed species (Bal et al., 2001). The success of raised bog restoration measures is mainly evaluated on the basis of the development of a *Sphagnum*-dominated vegetation, as well as the presence of characteristic *Sphagnum* and vascular plant species. Evaluations of restoration measures including fauna diversity have, however, been rare and have usually dealt with only one specific taxonomic group and one specific area (e.g. Utschick, 1990; König, 1992; Mossakowski and Främbs, 1993; Irmler et al., 1998). Buttler et al. (1996) showed that the testate amoebae fauna of raised bogs can recover rapidly and fully, regardless of the initial condition of the cutover surface. Since most restoration projects do not include a monitoring programme, it is generally unknown whether they have had any effects on the fauna, whether positive or negative. Also, little attention is being paid to fauna diversity in the planning of management measures.

To assess the effects of restoration measures on fauna and identify the key factors in successful conservation and restoration of fauna, a study of aquatic macroinvertebrates in Dutch raised bog areas was started. Aquatic macroinvertebrates were chosen, because most measures in raised bog restoration are focussed on water quantity and quality. The present study compared species assemblages between (1) water bodies created by rewetting measures aimed at the restoration of raised bog habitats and (2) water bodies which have not been subject to restoration measures, but are remnants of former peat cuttings and trenches used for buckwheat culture, abandoned in the first half of the twentieth century. These two groups of water bodies will be referred to as restoration sites and remnant sites, respectively. Conservation and restoration in raised bog areas should include not only the characteristic bog species, but also those species which are nowadays more or less dependent on raised bog areas for their survival in the Netherlands. Therefore, the present paper does not focus only on species characteristic of pristine bogs, but also takes into account the present distribution of non-characteristic macroinvertebrate species.

The present paper addresses the question whether remnant and restoration sites differ in species assemblage, species richness, and the numbers of characteristic and rare fauna species. A second question was whether the numbers of characteristic and rare species in these water bodies could be related to the presence of a characteristic vegetation and to the time that had elapsed since restoration measures were taken.

Materials and methods

Sampling sites

Aquatic macroinvertebrates were sampled at 47 sites in 7 raised bog areas (Figure 1). Sampling sites were chosen to include most of the various types of water body present. The water bodies sampled differed in age, size, water and substrate quality, vegetation composition and structure. Twenty-seven of the water bodies sampled were created by rewetting measures, 20 were remnants of former peat cutting or trenches used in buckwheat culture, which had been in existence for more than 50 years and had not been subject to bog restoration measures. These sites were in different stages of secondary succession.

Sampling method

Macroinvertebrates were sampled using a 20×30 cm pond net with $^1/_2$ mm mesh size. Most samples con-

Figure 1. Locations of raised bog areas in the Netherlands at which samples were taken. 1. Fochteloërveen (0/4), 2. Dwingelderveld (8/0), 3. Bargerveen (1/10), 4. Haaksbergerveen (1/9), 5. Korenburgerveen (4/0), 6. Mariapeel (0/4), 7. Tuspeel (6/0). Figures in brackets are the numbers of remnant and restoration sites sampled at each of the areas.

sisted of a 1 m sweep starting from the substrate and more or less open water into more dense vegetation near the shore. If the water body only included open water, one or more longer sweeps were taken to collect at least 100 macroinvertebrate individuals in a sample. In very dense *Sphagnum* vegetation, 20 to 50 cm sweeps were made to avoid the pond net becoming clogged with *Sphagnum*. As fauna abundance is generally high in this dense vegetation, most of these small samples contained over 100 individuals, or even more than 1000. Only in two small remnant water bodies were fewer than 100 individuals caught.

Each site was sampled both in spring 1999 and autumn 1998 or 1999, except four temporary remnant water bodies, which could only be sampled in either spring or autumn. Samples were transported to the laboratory and stored until analysis at 4 °C. The collected material was washed over three sieves with 2, 1, and $^1/_2$ mm mesh sizes respectively and sorted in white trays. All macroinvertebrates were identified to species level if possible, except Coleoptera larvae and Oligochaetes, which were excluded from the data analysis.

Environmental variables

The year in which the restoration sites had been rewetted was derived from management reports or provided by the local manager. Variables assessed in summer for all sampling sites included the presence of open water, *Sphagnum*, floating leaves of higher plant species, trees and muddy sediment, as well as the mean *Sphagnum* density in numbers of capituli per dm^2, and whether the water body was permanent or temporary. In spring, summer and autumn field assessments included the depth of the water body, surface area, electric conductivity and pH and samples of the surface water were taken. Samples were stored overnight at 4 °C, and turbidity, pH and alkalinity were measured the next day. After 1 mg citric acid per 5 ml of water had been added, samples were stored at –20 °C until analysis. The concentrations of the following substances were determined colorimetrically; NO_3^- according to Grasshoff and Johannsen (1977), NH_4^+ according to Kamphake et al. (1967), PO_4^{3-} according to Henriksen (1965). Cl^- according to O'Brien (1962). Na and K were determined with a Technicon flame photometer. Ca, Mg, Fe, Al, P and S were measured by inductively coupled plasma emission spectrometry (Jarell Ash Plasma 200, Instrumentation Laboratory). Total inorganic carbon in surface water was measured once with an 'Oceanography International' model 0525 HR infrared carbon analyser on autumn samples. Oxygen content was determined once, using the Winkler titration (Drew and Robertson, 1974; Carpenter, 1965) on samples collected in the autumn during daytime. For those environmental variables that were measured more than once, average values were used in the data analyses.

Classification of macroinvertebrate species

Macroinvertebrate species were considered to be characteristic of raised bogs if they were listed in literature as acidophilous, acidobiontic, tyrphophilous, tyrphobiontic or typical of raised bogs. These data and data on species rareness in the Netherlands were taken from Peus (1923), Nieser (1982), Geijskes and Van Tol (1983), Drost et al. (1992), Higler (1995), Duursema (1996), Bos and Wasscher (1997), Wasscher et al. (1998), Smit and Van der Hammen (2000), Nijboer and Verdonschot (2001) and from information provided by an expert (Dr H.K.M. Moller Pillot, pers. comm.). Red Lists were available for Turbellaria, Odonata, Ephemeroptera and Trichoptera (Wasscher

Table 1. Plant species found at sampling sites and scores assigned to them.

Plant species	Score
Sphagnum magellanicum, S. papillosum, S. rubellum, permanent floating raft with *Sphagnum* sp.	10
Calluna vulgaris, Erica tetralix, Eriophorum angustifolium, Eriophorum vaginatum, Menyanthes trifoliata, Rhynchospora alba, Sphagnum denticulatum, Utricularia minor	5
Agrostis canina, Carex rostrata, Hydrocotyle vulgaris, Potamogeton natans, Potentilla palustris, Sphagnum cuspidatum	2.5
Azolla filiculoides, Betula sp., filamentous green algae, *Juncus effusus, Molinia caerulea, Phragmites australis, Quercus robur, Salix* sp.	0

et al., 1998; Verdonschot et al., in prep.). For Coleoptera, the provisional Red List presented by Drost et al. (1992) was used.

Vegetation and macroinvertebrates indices

The species composition of the vegetation in each water body and the adjacent vegetation was assessed by estimating plant species cover, using cover class numbers 1 to 7 for the classes sporadic, rare, occasional, frequent, abundant, co-dominant and dominant from the scale proposed by Tansley (1946). Each plant species was assigned a score based on rareness, trend and desirability from the point of view of raised bog restoration (Table 1). Ten points were assigned for the hummock-building *Sphagnum* species *S. magellanicum, S. papillosum,* and *S. rubellum* and for a permanent floating raft with *Sphagnum* species. Five points were assigned for species which are rare and declining in the Netherlands (Van der Meijden, 1996) and are characteristic of raised bog vegetation. Undesirable species like *Betula* sp. and *Molinia caerulea* were assigned no points. Relatively common, but not undesirable species were assigned 2.5 points. A Vegetation Quality Score (VQS) was calculated for each sampling site by the sum of the species cover class multiplied by the species score and dividing this by the sum of all species cover class numbers.

$$VQS = \frac{\sum_{i=1}^{n} (\text{score of species}_i \ {}^{*}\text{cover class}_i)}{\sum_{i=1}^{n} \text{cover class}_i}$$

Based on Foster (1990), a Fauna Species Quality Score (FSQS) was calculated for each sampling site. A similar procedure has also been applied by e.g. Painter (1999) and Oertli et al. (2002). All species were assigned a species score, depending on their rareness class in the Netherlands. The species scores of very common, common, fairly common, fairly rare, rare and very rare species were 1, 2, 4, 8, 16 and 32 respectively. For characteristic species, the species score was multiplied by two. The FSQS of a site was the average score of all species present.

$$FSQS = \frac{\sum_{i=1}^{n} \text{score of species}_i}{\text{total number of species}}$$

Data analysis

Data on the presence of macroinvertebrate species in the spring and autumn samples were pooled for each of the 47 sites. Correspondence Analysis (CA) of these data was performed in Canoco for Windows version 4.0 (Ter Braak and Smilauer, 1998). The significance of each environmental variable was tested with the Monte Carlo resampling procedure (500 permutations). Cumulative species richness curves were based on averages of 50 random sorts of the sampling sites using BioDiversityProfessional Beta 1 (McAleece, 1997).

To determine whether correlations existed between VQS or site age and the numbers of rare and characteristic macroinvertebrate species or FSQS, Pearson correlation coefficients and their significance were calculated using SPSS. Significance of differences in the numbers of rare and characteristic macroinvertebrate species, FSQS and VQS between remnant and restoration sites was tested using the Student T-test.

Results

Fauna species assemblages

The correspondence analysis plot of the sampling sites is shown in Figure 2. The site scores were calculated

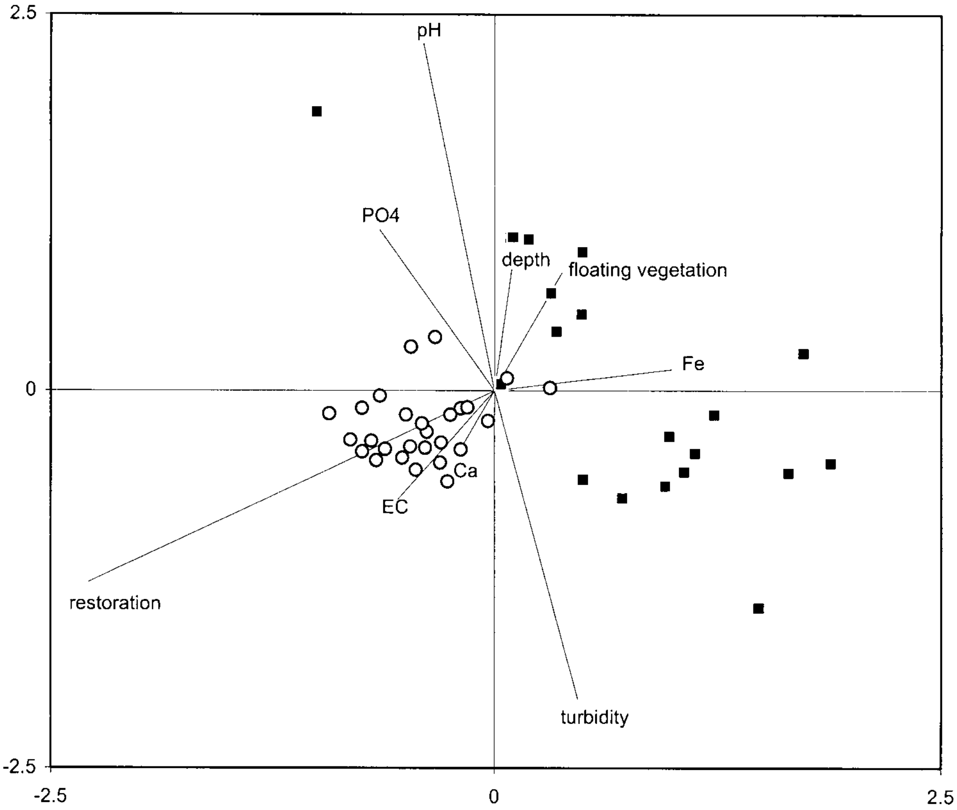

Figure 2. Correspondence Analysis plot of sampling sites based on the presence of macroinvertebrate species. Significant environmental variables are shown as lines. Open circles represent restoration sites and filled squares represent remnant sites.

from the macroinvertebrate species presence data only. Remnant sites and restoration sites were clearly separated on the first and second CA-axis, which explained 7.4% and 6.4% of the variation in species data, respectively. Restoration sites were plotted very close together compared to remnant sites. This indicates that the degree of variation in species assemblages was relatively low at the restoration sites.

When the variable restoration vs. remnant site was excluded, 66.0% of the total variance in species data could be explained by all other environmental variables. Adding this variable resulted in an increase of total explained variation of 2.5%. Restoration vs. remnant alone explained 6.0% of the total species variation. This is equal to 8.8% of the variance explained by all environmental variables and to 81% of the variation explained by the first CA-axis. After the deletion of alkalinity, total P and Na – because of high correlations with pH, PO_4 and Cl respectively – the variables restoration vs. remnant site, pH, electric conductivity, Ca, Fe, PO_4, depth, presence of floating leaves and turbidity contributed significantly ($p < 0.05$) to explaining the variation in fauna data. These significant variables together accounted for 34.5% of the variation in fauna data. These variables were plotted inert in the CA-plot in Figure 2.

Species richness

At the 47 sampling sites a total of 149 macroinvertebrate species sampled were found (Table 2). Of these, 133 species were found at the 20 remnant sites, versus 100 species at the 27 restoration sites. Eighty-four species were found at both remnant and restoration sites. Figure 3 shows cumulative species richness curves for remnant sites and restoration sites. Apart from the difference in total species richness, the difference in the shape of the curves is remarkable. Both curves are still rising at their ends, but the slope of the remnant sites curve is steeper than that of the restoration sites curve. Species richness per site did not differ sig-

Table 2. Numbers (N) and relative numbers of macroinvertebrate species found at all sampling sites together, remnant sites and restoration sites, and numbers of species found at both remnant sites and restoration sites, for different classes of rareness in the Netherlands. n = number of sampling sites.

Rareness class	All sites n = 47		Remnant sites n = 20		Restoration sites n = 27		Species shared
	N	%	N	%	N	%	N
Very common	37	*24.8*	33	*24.8*	28	*28.0*	24
Common	37	*24.8*	33	*24.8*	26	*26.0*	22
Fairly common	34	*22.8*	31	*23.3*	23	*23.0*	20
Fairly rare	29	*19.5*	24	*18.0*	18	*18.0*	13
Rare	8	*5.4*	8	*6.0*	5	*5.0*	5
Very rare	4	*2.7*	4	*3.0*	0	*0.0*	0
Total species number	149	*100.0*	133	*100.0*	100	*100.0*	84

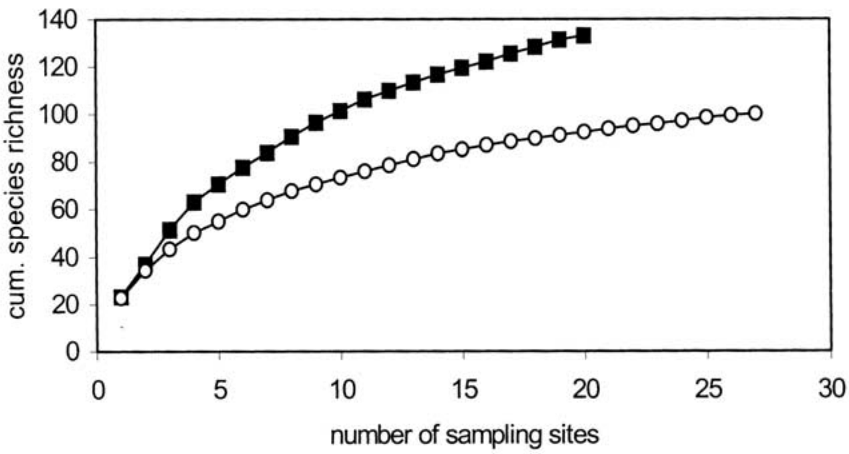

Figure 3. Cumulative macroinvertebrate species richness curves of 27 restoration sites and 20 remnant sites composed of averages of 50 random sorts of sampling sites. Open circles for restoration sites and filled squares for remnant sites.

Table 3. Averages (± sd) of the total numbers of individuals, species richness, numbers of characteristic and more or less rare characteristic species (CR in Table 4), Fauna Species Quality Scores (FSQS) and Vegetation Quality Scores (VQS) of the sampling sites. Significance of the differences between remnant and restoration sites is indicated as the P-values in the T-test. *n* = number of sampling sites.

	Remnant sites n = 20	Restoration sites n = 27	T-test *p*
Individuals/sampling site	576 ± 388	1276 ± 932	*0.001*
Species richness	24.0 ± 15.4	22.7 ± 5.8	0.722
Characteristic species	6.7 ± 4.3	5.1 ± 3.3	0.153
Rare characteristic species	3.6 ± 2.5	2.4 ± 2.1	0.063
FSQS	6.4 ± 2.0	4.5 ± 1.8	*0.001*
VQS	3.6 ± 1.8	2.5 ± 1.8	*0.041*

nificantly between the remnant and restoration sites. However, the number of individuals collected per site was significantly lower at the remnant sites (Table 3).

Species rareness, characteristic species, quality scores, and Red-Listed species

Thirty-six of the 41 fairly rare, rare, and very rare species were sampled at the remnant sites (Table 2), while the restoration sites yielded only 23 more or less rare species. All 12 rare and very rare species found were present at at least one of the remnant sites, whereas 5 of them were found at restoration sites. Species more or less common in the Netherlands represented 72.9% (97 species) of the total number of species at the remnant sites and 77.0% (77 species) at the restoration sites.

Species characteristic of raised bog systems or included in the Red List are listed in Table 4. Thirty-six of the 149 species collected are more or less characteristic of water bodies in raised bog systems. Thirty-four of them were found at the remnant sites and 24 at the restoration sites. Of the 11 fairly common characteristic species, only 1 species was not found at the restoration sites, while 7 of the 19 fairly rare characteristic species were not found. Two of the 4 rare and none of the 2 very rare characteristic species were found at the restoration sites.

Some of the characteristic species were frequently found, most of these being fairly common in the Netherlands (Table 4). The average numbers of characteristic species and of fairly rare, rare, and very rare characteristic species (CR in Table 4) sampled per site were higher at the remnant sites, although the difference was not statistically significant (Table 3). The Fauna Species Quality Score and the Vegetation Quality Score were significantly higher at the remnant sites.

Of the 149 species collected, 11 are on the Red List. Seven of them are characteristic of raised bogs. The 4 non-characteristic Red-Listed species were only found at 3 different remnant sites. Both at remnant sites and restoration sites 5 characteristic Red-Listed species were found.

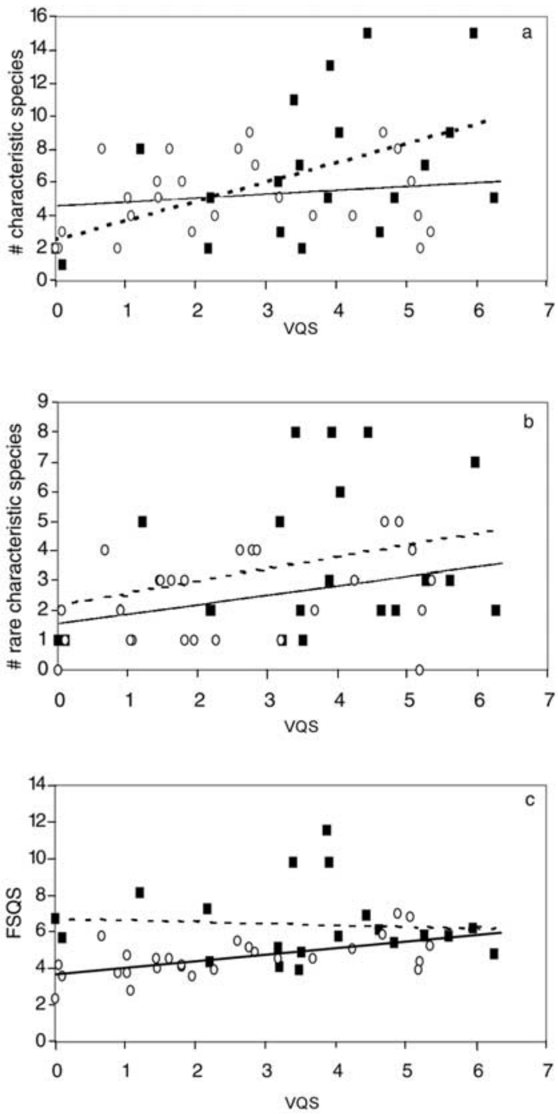

Figure 4. Relation between the numbers of a) characteristic species and b) more or less rare characteristic species (CR in Table 4) and c) Fauna Species Quality Scores (FSQS), and the Vegetation Quality Scores (VQS) for 20 remnant sites and 27 restoration sites. Significant correlations are indicated by bold trend lines, the others by ordinary lines. Uninterrupted trend lines and open circles are used for restoration sites, dotted lines and filled squares for remnant sites. For explanation of statistics see text.

Correlations with VQS and site age

For the 20 remnant sites, the number of characteristic species per site was significantly correlated with VQS (r = 0.49, $p = 0.030$; Figure 4). The number of more or less rare characteristic species (CR in Table 4) and FSQS were not significantly correlated with VQS (r = 0.28, $p = 0.235$ and r = –0.09, $p = 0.709$, respectively). For the 27 restoration sites, only the FSQS was correlated with the VQS (r = 0.60, $p = 0.001$), while no significant correlation was found between VQS and the number of characteristic and rare characteristic species (r = 0.20, $p = 0.329$ and r = 0.373, $p = 0.055$, respectively).

Table 4. Numbers of sampling sites at which characteristic species (C), more or less rare characteristic species (CR), and Red-Listed species (RL) were found. The taxonomic group to which species belong is abbreviated: Hydrachnidia (hyd), Chaoboridae (cha), Chironomidae (chi), Coleoptera (col), Cylindrotomidae (cyl), Heteroptera (het), Odonata (odo), and Trichoptera (tri). Red List (RL) classes are: strongly threatened (1), threatened (2), and vulnerable (3). Rareness classes are fairly common (fc), fairly rare (fr), rare (r), and very rare (vr). Tyrphobiontic (tb), tyrphophilous (tp), acidobiontic (ab) and acidophilous (ap). n = number of sampling sites.

Species name	Taxonomic group	C	CR	Rareness class	RL class	tb	tp	ab	ap	All sites n = 47	Remnant n = 20	Restoration n = 27
										numbers of sampling sites		
Ilybius aenescens	col	×	×	fr		×				11	2	9
Acilius canaliculatus	col	×	×	fr			×			13	6	7
Agabus congener	col	×	×	r			×			3	3	0
Berosus luridus	col	×	×	fr			×			1	0	1
Bidessus spec.	col	×	×	fr	1		×			4	3	1
Enochrus affinis	col	×		fc			×			13	9	4
Helophorus flavipes	col	×	×	r			×			2	2	0
Hydroporus gyllenhalii	col	×	×	fr				×		5	5	0
Hydroporus melanarius	col	×	×	fr				×		3	3	0
Hydroporus obscurus	col	×	×	fr				×		11	7	4
Hydroporus pubescens	col	×		fc				×		8	6	2
Hydroporus tristis	col	×		fc				×		18	14	4
Arrenurus stecki	hyd	×	×	fr					×	18	5	13
Hydroporus scalesianus	col	×	×	fr	2				×	4	2	2
Nartus grapii	col	×	×	fr	2				×	1	1	0
Oxus nodigerus	hyd	×	×	r					×	5	4	1
Agrypnia obsoleta	tri	×	×	fr	3					3	0	3
Arrenurus neumani	hyd	×	×	fr						1	1	0
Ceriagrion tenellum	odo	×	×	fr						8	4	4
Coenagrion lunulatum	odo	×		fc	1					14	1	13
Cymatia bonsdorffi	het	×		fc						14	1	13
Enochrus ochropterus	col	×	×	fr						11	5	6
Gerris gibbifer	het	×	×	fr						1	1	0
Graphoderus zonatus	col	×	×	fr						1	1	0
Hebrus ruficeps	het	×		fc						9	5	4
Hesperocorixa castanea	het	×	×	fr						4	4	0
Hydroporus umbrosus	col	×		fc						16	7	9
Laccophilus ponticus	col	×	×	vr	1					1	1	0
Lasiodiamesa spec.	chi	×	×	vr						4	4	0
Leucorrhinia dubia	odo	×		fc	3					4	2	2
Leucorrhinia rubicunda	odo	×		fc						18	5	13
Macropelopia adaucta	chi	×		fc						4	4	0
Micropsectra fusca	chi	×	×	fr						3	2	1
Mochlonyx fuliginosus	cha	×	×	r						8	6	2
Phalacrocera replicata	cyl	×	×	fr						24	6	18
Psectrocladius platypus	chi	×		fc						16	6	10
Cybister lateralimarginalis	col			fc	2					1	1	0
Hagenella clathrata	tri			vr	3					1	1	0
Limnephilus marmoratus	tri			fr	3					1	1	0
Limnephilus nigriceps	tri			vr	2					1	1	0
Total numbers of species												
Remnant sites		34	23		10	1	5	5	4	38	38	
Restoration sites		24	14		5	1	4	3	3	24		24
All sites		36	25		11	1	6	5	4	40		

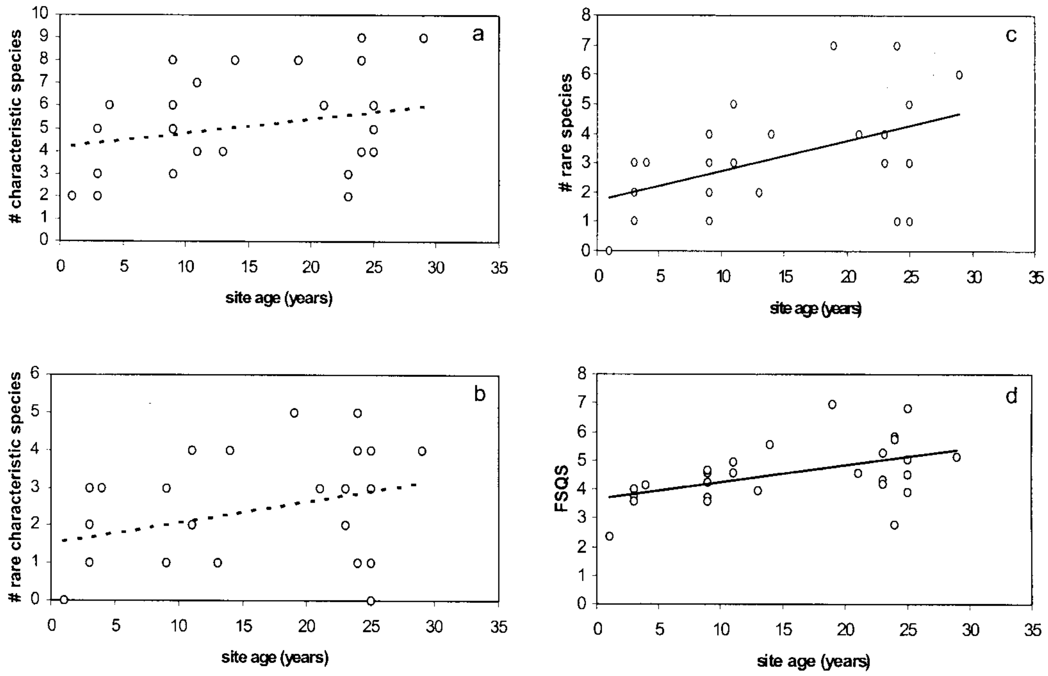

Figure 5. Numbers of a) characteristic species, b) more or less rare characteristic species (CR in Table 4) and c) more or less rare species and d) Fauna Species Quality Scores (FSQS) for the 27 restoration sites, plotted against site age. Significant correlations are indicated by uninterrupted trend lines, the others by dotted trend lines. For explanation of statistics see text.

No significant correlation was found between site age and the number of characteristic or rare characteristic species at the restoration sites (r = 0.25, $p = 0.214$ and r = 0.33, $p = 0.092$, respectively), although a positive trend was found (Figure 5). However, FSQS and the number of fairly rare and rare species per site were correlated with the number of years elapsed after rewetting measures were taken (r = 0.50, $p = 0.009$ and r = 0.48, $p = 0.012$, respectively).

Discussion

Macroinvertebrate species assemblages appear to differ between restoration sites and remnant sites. Both restoration sites and remnant sites were inhabited by a number of characteristic, rare and Red Listed macroinvertebrate species. However, larger numbers of characteristic species and rare species were found at the remnant sites, resulting in the higher Fauna Species Quality Score (FSQS) at the remnant sites. The cumulative species richness was also high compared to the restoration sites and more than a quarter of the characteristic species was only found at the remnant sites. This difference is strengthened by the fact that the numbers of individuals collected were significantly lower at the remnant sites. What could be the causes of these differences between remnant sites and restoration sites?

Important factors structuring aquatic macroinvertebrate species assemblages of inland waters in the Netherlands are salinity, current velocity, dimensions of water bodies, duration of drought periods, acidity and trophic state (Leuven et al., 1987a and 1987b; Van der Hammen, 1992; Verdonschot et al., 1992). Some of these, or related, variables significantly explained the variation in the species assemblages within the group of remnant sites as well as within the group of restoration sites, but not clearly between these two groups of sites. Besides these factors related to habitat quality, site age and colonisation time may be important, as Painter (1999) and Fairchild et al. (2000) showed for aquatic beetles. Site age was not analysed in our correspondence analysis, as the age of most of the remnant sites was unknown. However, it is important to know whether age is an important causal factor and what restoration measures will contribute in due time to the conservation and restoration of a complete species spectrum within the Netherlands.

The FSQS of restoration sites was found to increase with site age. This was mainly due to the correlation between the numbers of fairly rare and rare species and the site age. The numbers of characteristic and rare characteristic species were not significantly correlated with the site age. The age of the oldest restoration site sampled in the present study was 29 years. The restoration sites might be expected to become recolonized by larger numbers of characteristic and rare species after a longer time period, on the conditions that (1) adjacent populations of these species are present and (2) the sites meet the habitat requirements of the species. The presence of adjacent populations is important in the highly fragmented landscape of the Netherlands (Den Boer, 1990; De Vries, 1996), especially for raised bog species and a substantial number of rare species, as raised bog areas have become rare and a considerable number of species are hardly able to disperse over long distances. Biggs et al. (2001) found that the restoration of the river Cole (UK) was successful because its upper reaches and stagnant water bodies along the river harboured many species, which were able to recolonize the river after restoration. This stresses the importance of remnant sites as refugia until restoration sites have been recolonized by the species in question.

Regarding the habitat requirements of the various macroinvertebrate species, further analysis of the ecological traits of the macroinvertebrates are necessary to understand differences in species assemblages within and between remnant and restoration sites. The present data do not allow the conclusion that restoration measures will after some time result in suitable habitats for the species diversity, especially for the characteristic species, present at the remnant sites. The cumulative species richness of remnant sites was relatively high, whereas species richness per site did not differ between the remnant and restoration sites. This means that the remnant sites included much more variation in species assemblages, which is also indicated by the different ranges of site scores in the CA-plot. Extrapolation of the cumulative species richness curve indicates that more restoration sites will not result in a major increase in species numbers. So far, rewetting measures in various initial situations have resulted in a habitat for a limited number of fauna species, including only some of the characteristic raised bog species. Currently, a considerable number of characteristic and rare species are still dependent on remnant sites for their survival in raised bog areas, and in the Netherlands as a whole.

The number of characteristic macroinvertebrate species was not clearly related to the presence of a characteristic raised bog vegetation. Sites with a successful restoration of a characteristic raised bog vegetation (high VQS) do not necessarily have larger numbers of characteristic macroinvertebrate species. The VQS of the remnant sites with the largest numbers of more or less rare characteristic fauna species was moderate. The dominant plant species at these sites were *Betula* sp., *Molinia caerulea* and *Sphagnum cuspidatum*, with some *Eriophorum angustifolium*. These sites are actually the only known find-spots in Western Europe of the very rare and characteristic chironomid species *Lasiodiamesa gracilis* (cf. Brundin, 1966).

What do these results mean for restoration management in raised bog areas? Rewetting is necessary to restore hydrological and biogeochemical processes of raised bog systems in order to restore a characteristic hummock-hollow vegetation. If a restoration site initially consisted of cutover bare peat, the establishment of some characteristic plant and fauna species is a nice result of the restoration measures taken. However, it is worse when the area initially included remnant sites with some characteristic species, which are now substituded by a species assemblage like all other restoration sites, excluding previously present characteristic and rare species. Therefore, raised bog restoration should not focus everywhere on creating suitable conditions only for the hummock-hollow vegetation type.

Studies on several groups of aquatic macroinvertebrates in Dutch raised bog areas (Verberk et al., 2001) and in relatively pristine raised bog systems in Ireland and Estonia (De Leeuw, 1986; Smits et al., 2002) show that characteristic species do not all occur in ombrotrophic raised bog centres. Although several characteristic species might only depend on e.g. large, open pools or shallow pools with dense *Sphagnum* vegetation in bog centres, other species need other elements of the raised bog system, like transitional habitats or water bodies with some water flow or the influence of minerotrophic water. In addition, several species depend on environmental conditions which only occur in gradients or need a combination of different habitats to complete the different stages in their life cycles (Verberk et al., 2001; Schouwenaars et al., 2002), or for longer-term survival in case of unfavourable periods in one or more of the present habitat types (Settele et al., 1996; pers. comm. Moller Pillot). Habitat diversity within an area can offer more suitable habitats, resulting in greater species richness (Harper et al., 1997). Thus, conservation and restoration of habitat diversity is necessary to meet the requirements of the species diversity of complete raised bog systems.

In conclusion, efforts to improve the success of restoration measures in raised bog areas need to focus first on the conservation of the present refugia of characteristic bog species or species that have become rare. Therefore, it is necessary to assess which species are present in the various habitat types, before any measures are taken. Such assessments should not neglect sites which do not seem very valuable on the basis of their vegetation composition. Next to the assessment of the present fauna species, it is important to know the habitat conditions that species depend on and the regional and local hydrological and biogeochemical processes causing these conditions. Just these processes are influenced by such restoration measures as building bunds and weirs to manipulate e.g. water table fluctuations and water flow patterns. This knowledge is essential in choosing the restoration strategy which will conserve populations in the short term and will restore characteristic flora and fauna species assemblages in the various parts of the raised bog system in the longer term (Schouten et al., 1998). In most cases, measures have to be phased in time and space, but the precise time scale to be used depends on the distribution and habitat requirements of the species concerned and on the progress of restoration and recolonization, as well as on the possible side-effects of measures. When monitoring has shown that the species concerned have colonized other parts of the area, (phased) measures can be taken to restore conditions for other target species to recover. Safeguarding the necessary habitat diversity during the restoration process and restoring different elements of the habitat diversity of complete raised bog systems will result in the characteristic fauna diversity being conserved and restored more successfully.

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References

Akkermann, R. 1982. Möglichkeiten und Zielsetzungen für eine Regeneration von Hochmooren – zoologisch betrachtet. *In:* Akkermann, R. (ed.), Regeneration von Hochmooren. Informationen zu Naturschutz und Landschaftspflege in Nordwestdeutschland. Band 3. pp. 151–163.

Bal, D., Beije, H.M., Fellinger, M., Haveman, R., van Opstal, A.J.F.M. and van Zadelhoff, F.J. 2001. Handboek Natuurdoeltypen. Ministerie van Landbouw, Natuurbeheer en Visserij, Wageningen. 832 pp.

Biggs, J., Fox, G., Whitfield, M., Williams, P., Sear, D. and Bray, S. 2001. River restoration – Is it worth it? Freshw. Biol. Ass. Newsl. 14: 1–3.

Bobbink, R., Hornung, M. and Roelofs, J.G.M. 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. J. Ecol. 86: 717–738.

Bos, F. and Wasscher, M. 1997. Veldgids Libellen. KNNV, Utrecht. 256 pp.

Brundin, L. 1966. Transantarctic relationship and their significance, as evidenced by chironomid midges – with a monograph of the subfamilies Podonominae and Aphroteniinae and the Austral Heptagyiae. Kungliga Svenska Vetenskapsakademiens handlingar. Series 4, band 11. Stockholm. 472 pp.

Buttler, A., Warner, B.G., Grosvernier, P. and Matthey, Y. 1996. Vertical patterns of testate amoebae (Protozoa: Rhizopoda) and peat-forming vegetation on cutover bogs in the Jura, Switzerland. New Phytol. 134: 371–382.

Carpenter, J.H. 1965. The Chesapeake Bay Institute technique for the Winkler dissolved oxygen method. Limnol. & Oceanogr. 10: 141–143.

Den Boer, P.J. 1990. The survival value of dispersal in terrestrial arthropods. Biol. Conserv. 54: 175–192.

De Leeuw, J.P.M. 1986. Een Onderzoek naar het Voorkomen en de Verspreiding van Aquatische Macro- en Microfauna in de Ierse Hoogvenen, deel 1: Macrofauna. Doctoraalverslag 206, Aquatische Oecologie, Katholieke Universiteit Nijmegen. 75 pp.

De Vries, H.H. 1996. Viability of Ground Beetle Populations in Fragmented Heathlands. Biological Station Wijster, Wageningen Agricultural University. 133 pp.

Drew, E.A. and Robertson, A.A. 1974. A simple field version of the Winkler determination of dissolved oxygen. New Phytol. 73: 793–796.

Drost, M.B.P., Cuppen, H.P.J.J., van Nieukerken, E.J. and Schreijer, M. (eds.). 1992. De Waterkevers van Nederland. Uitgeverij KNNV, Utrecht. 280 pp.

Duursema, G. 1996. Vennen in Drenthe, een Onderzoek naar Ecologie en Natuur op Basis van Macrofauna. Zuiveringsschap Drenthe, Assen. 140 pp.

Fairchild, G.W., Faulds, A.M. and Matta, J.F. 2000. Beetle assemblages in ponds: effects of habitat and site age. Freshw. Biol. 44: 523–534.

Foster, G.N., Foster, A.P., Eyre, M.D. and Bilton, D.T. 1990. Classification of water beetle assemblages in arable fenland and ranking of sites in relation to conservation value. Freshw. Biol. 22: 343–354.

Geijskes, D.C. and Van Tol, J. 1983. De Libellen van Nederland. Koninklijke Nederlandse Natuurhistorische Vereniging, Hoogwoud. 368 pp.

Göttlich, K. 1980. Moor- und Torfkunde. E. Schweizerbart'sche Verlagsbuchhandlung Stuttgart. 338 pp.

Grasshoff, H. and Johanssen, H. 1977. A new sensitive method for determination of ammonia in seawater. Water Res. 2: 516.

Harper, D., Mekotova, J., Hulme, S., White, J. and Hall, J. 1997. Habitat heterogeneity and aquatic macroinvertebrate diversity in floodplain forests. Global Ecol. & Biogeogr. Lett. 6: 275–285.

Henriksen, A. 1965. An automated method for determining low-level concentrations of phosphate in fresh and saline waters. Analyst 90: 29–34.

Higler, L.W.G. 1995. Lijst van kokerjuffers (Trichoptera) in Nederland met opmerkingen over uitgestorven en bedreigde soorten. Entomol. Ber. 55: 149–156.

Irmler, U., Müller, K. and Eigner, J. 1998. Das Dosenmoor – Ökologie eines regenerierenden Hochmoores. Faunistisch-ökologische Arbeitsgemeinschaft, Kiel. 283 pp.

Kamphake, L.H., Hannah, S.H. and Cohen, J.M. 1967. Automated analysis for nitrate by hydrazine reduction. Water Res. 1: 206.

König, A. 1992. Die Libellenfauna im Abbaugebiet Haidauer Ried des Wurzacher Riedes. Telma 22: 109–122.

Lamers, L.P.M., Farhoush, C., van Groenendael, J.M. and Roelofs, J.G.M. 1999. Calcareous groundwater raises bogs; the concept of ombrotrophy revisited. J. Ecol. 87: 639–648.

Lamers, L.P.M., Tomassen, H.B.M. and Roelofs, J.G.M. 1998a. Sulfate-induced eutrophication and phytotoxicity in freshwater wetlands. Envir. Sci. & Technol. 32: 199–205.

Lamers, L.P.M., van Roozendaal, S.M.E. and Roelofs, J.G.M. 1998b. Acidification of freshwater wetlands: combined effects of non-airborne sulfur pollution and desiccation. Water, Air & Soil Poll. 105: 95–106.

Leuven, R.S.E.W., van der Velden, J.A., Vanhemelrijk, J.A.M. and van der Velde, G. 1987a. Impact of acidification on chironomid communities in poorly buffered waters in The Netherlands. Entomologica scandinavica Supplements 29: 269–280.

Leuven, R.S.E.W., Vanhemelrijk, J.A.M. and van der Velde, G. 1987b. The distribution of Trichoptera in Dutch soft waters differing in pH. *In:* Bournaud, M. and H. Tachet (eds.), Proc. 5th Int. Symp. on Trichoptera. Junk Publishers, Dordrecht, pp. 359–365.

McAleece, N. 1997. Biodiversity Professional Beta 1. The Natural History Museum, London and The Scottish Association for Marine Science, UK.

Mossakowski, D. and Främbs, H. 1993. Carabiden als Indikatoren der Auswirkungen von Wiedervernässerungsmassnahmen auf die Fauna im Leegmoor. Natursch. Landschaftspfl. Nieders. 29: 79–114.

Nieser, N. 1982. De Nederlandse water- en oppervlaktewantsen (Heteroptera: Nepomorpha en Gerromorpha). Wetensch. Med. K.N.N.V. 155: 1–103.

Nijboer, R.C. and Verdonschot, P.F.M. (eds.). 2001. Zeldzaamheid van de Macrofauna van de Nederlandse Binnenwateren. Werkgroep Ecologisch Waterbeheer, themanummer 19. 77 pp.

RIVM. 2001. Natuurbalans 2001. Kluwer, Alphen aan den Rijn. 189 pp.

O'Brien, J. 1962. Automatic analysis of chlorides in sewage wastes. Engineering 33: 670–672.

Oertli, B., Auderset Joye, D., Castella, E., Juge, R., Cambin, D. and Lachavanne, J.-B. 2002. Does size matter? The relationship between pond area and biodiversity. Biol. Conserv. 104: 59–70.

Painter, D. 1999. Macroinvertebrate distributions and the conservation value of aquatic Coleoptera, Mollusca and Odonata in the ditches of traditionally managed and grazing fen at Wicken fen, UK. J. Appl. Ecol. 36: 33–48.

Peus, F. 1923. Die Tierwelt der Moore. Handbuch der Moorkunde III. Bornträger verlag, Berlin. 277 pp.

Schouten, M.G.C., Schouwenaars, J.M., Esselink, H., Lamers, L.P.M. and van der Molen, P.C. 1998. Hoogveenherstel in Nederland – droom en werkelijkheid. *In:* Bobbink, R., Roelofs, J.G.M. and Tomassen, H.B.M. (eds.), Effectgerichte Maatregelen en Behoud Biodiversiteit in Nederland. pp. 93–113. Symposiumverslag. Aquatische Oecologie en Milieubiologie, Katholieke Universiteit Nijmegen.

Schouwenaars, J.M., Esselink, H., Lamers, L.P.M. and van der Molen, P.C. 2002. Ontwikkelingen en Herstel van Hoogveensystemen – Bestaande Kennis en Benodigd Onderzoek. Expertisecentrum LNV, Wageningen. 188 pp.

Settele, J., Margules, C., Poschlod, P. and Henle, K. (eds.). 1996. Species Survival in Fragmented Landscapes. Kluwer, Dordrecht. 381 pp.

Smit, H. and van der Hammen, H. 2000. Atlas van de Nederlandse watermijten (Acari: Hydrachnidia). Ned. Faun. Med. 13: 1–272.

Smits, M.J.A., van Duinen, G.A., Bosman, J.G., Brock, A.M.T., Javois, J., Kuper, J.T., Peeters, T.M.J., Peeters, M.A.J. and Esselink, H. 2002. Species richness in a species poor system: aquatic macroinvertebrates of Nigula raba, an intact raised bog system in Estonia. Proc. Int. Peat Symp., Pärnu, September 2002, pp. 283–291.

Tansley, A.G. 1946. Introduction to Plant Ecology. Allen and Unwin, London. 260 pp.

Ter Braak, C.J.F. and Smilauer, P. 1998. CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4). Microcomputer power. Ithaca, New York. 351 pp.

Utschick, H. 1990. Nachtfalter (Lepidoptera, Macroheterocera) als Bioindikatoren für Regenerationsprozessen in abgetorfter Hochmooren. Telma 20: 125–141.

Van der Hammen, H. 1992. De Macrofauna van het Oppervlaktewater van Noord-Holland. Thesis University of Nijmegen. Provincie Noord-Holland, Dienst Ruimte en Groen, Haarlem. 256 pp.

Van der Meijden, R. 1996. Heukels Flora van Nederland. Wolters-Noordhoff, Groningen. 676 pp.

Verberk, W.C.E.P., van Duinen, G.A., Peeters, T.M.J. and Esselink, H. 2001. Importance of variation in watertypes for water beetle fauna (Coleoptera) in Korenburgerveen, a bog remnant in The Netherlands. Proc. Exp. & Appl. Entomol., N.E.V., Amsterdam, 12, pp. 121–128.

Verdonschot, P.F.M., Higler, L.W.G., van der Hoek, W.F. and Cuppen, J.G.M. 1992. A list of macroinvertebrates in Dutch water types: a first step towards an ecological classification of surface waters based on key factors. Hydrobiol. Bull. 25: 241–259.

Verdonschot, P.F.M., Higler, L.W.G., Nijboer, R.C. and van den Hoek, T.H. in prep. Naar een Doelsoortenlijst van Aquatische Macrofauna in Nederland: Platwormen (Tricladida), Steenvliegen (Plecoptera), Haften (Ephemeroptera) en Kokerjuffers (Trichoptera). Alterra, Wageningen.

Verhoeven, J.T.A. (ed.). 1992. Fens and Bogs in The Netherlands: Vegetation, History, Nutrient Dynamics and Conservation. Kluwer, Dordrecht. 490 pp.

Wasscher, M., Keijl, G.O. and van Ommering, G. 1998. Bedreigde en Kwetsbare Libellen in Nederland. Toelichting op de Rode Lijst. IKC, Wageningen. 42 pp.

Wheeler, B.D. and Shaw, S.C. 1995. Restoration of Damaged Peatlands. HMSO, London. 211 pp.