Changes in macroinvertebrate richness and diversity following large scale rewetting measures in a heterogeneous bog landscape

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Restoration measures in raised bog remnants frequently include the construction of dams, intended to retain rainwater and decrease fluctuations in the water table. However, comparative research in various bog remnants has provided strong indications that there are risks for macroinvertebrates. Risks include (i) rapid changes causing a disturbance, and (ii) similar changes at a large scale leading to a loss of heterogeneity, and consequently to a loss of species. This paper directly examines the risks associated with rewetting measures in bog remnants by investigating and comparing the macroinvertebrate assemblages in the same area before and after measures took effect. At the scale of a single water body, species numbers mainly increased in water bodies that were not impacted by measures. Species numbers did not change in impacted water bodies. Moreover, the cumulative number of species declined in the rewetted parts, indicating that in general everywhere the same species benefited from the changes. This homogenisation of the invertebrate assemblages was also evident at the scale of the entire reserve. On average, abundant species increased, while scarce species decreased. These results highlight the importance of heterogeneity. Especially minerotrophic conditions proved to be important. Therefore, restoration of the regional hydrology is of vital importance to the conservation and restoration of macroinvertebrate diversity.

Keywords: regional hydrology, minerotrophic conditions, homogenisation, frequency-abundance, restoration management

Raised bogs are threatened ecosystems in the Netherlands. Restoration measures focus on restoring conditions for Sphagnum growth, which is a necessary prerequisite for the restoration of raised bog ecosystems. Therefore, current restoration plans frequently involve the construction of dams, intended to retain rain water and decrease fluctuations in the water table. However, comparative research in various bog remnants on macroinvertebrates has shown that large scale rewet-
ting of peat extraction areas only partly restores the macroinvertebrate assemblages (Van Duinen et al. 2003). Many rare and characteristic species are still absent in rewetted sites after 30 years, even though source populations may be present in the same bog remnant. This may be attributed to low dispersal capacity of characteristic species, or -more alarming- to an incomplete restoration of the conditions needed by these species. In contrast, non-rewetted sites still harboured many characteristic species (Van Duinen et al. 2003). This comparative research provided a strong indication that there may be risks involved in the restoration of remnants where rare and characteristic species are still present. These risks can be (i) rapid changes causing a disturbance (shock effects) species cannot cope with, and (ii) similar changes over a large scale leading to a loss of variation between patches (loss of heterogeneity) and consequently to a loss of species. These risks are enhanced for characteristic species as they generally occur either in low densities, or very locally, or both (thus contributing to the need to take restoration measures) and because characteristic species usually depend on specific patches.

This paper directly examines the risks associated with rewetting measures in bog remnants by investigating and comparing the macroinvertebrate assemblages in the same area before and after measures took effect. Specifically, we are interested in the effect of restoration measures on: 1. species richness and diversity per water body (alpha diversity), 2. cumulative species richness in bog pools (beta diversity), and 3. changes in frequency of occurrence and abundance of all species in the area (gamma diversity).

**METHODS**

**Data collection**

The water bodies sampled are located in the heterogeneous bog remnant Korenburgerveen (described in detail by Verberk et al. (2001, 2004)). In total 44 water bodies were sampled, belonging to different water types and distributed throughout the remnant (Fig. 1). Water bodies were sampled in 2000-2002 before measures took effect. In 2004, after the measures were taken, all water bodies were resampled. Samples were collected using a standard pond net of 30 x 20 cm with a mesh size of 0.5 mm. Sampling was confined to spring (April-May) and autumn (October-November). Data from spring and autumn were pooled. For each sampling site physical and chemical properties of the water body and local vegetation composition were measured and described. Verberk & Esselink (2004) give an extensive description of the research area, sample locations and a list of physical and chemical properties. Samples were washed and sorted in the laboratory. Tricladia, Hirudinea, Oligochaeta, Araneae, Crustacea, Odonata, Hemiptera, Coleoptera, Cylindrotomidae, Chaoboridae, Dixidae, Culicidae, Chironomidae and Trichoptera were identified to species level. Taxonomic groups which were not identified were excluded from further analysis.
Data analysis

To test the impact of the restoration measures, sample locations were grouped according to changes in environmental conditions, following restoration measures. Three types of changes were distinguished: water bodies were no or only minor changes had occurred (type 1) and water bodies impacted by rewetting measures, where a distinction was made between water bodies in wet forest (type 2) and bog pools (type 3). Type 2 and 3 could be further subdivided; Changes in water quality indicated a decrease (2a and 3a), an increase (2c and 3c) or no change (2b and 3b) in ground water influence.

To test whether changes in species diversity (Shannon index; Shannon 1948) and species richness (number of species) were related to compartment, water

![Figure 1. Subdivision of the research area into seven different compartments and the location of the sampled water bodies, subdivided in different types of change. Restoration measures (construction of dams and filling of ditches) are also indicated.](image-url)
type and type of change, an analysis of covariance (ANCOVA) was performed with time as a co-variable. In this ANCOVA, interactions between time * compartment, time * water type, and time * type of change were tested for significance.

To investigate changes in species richness on a larger spatial scale, species accumulation curves were constructed, based on averages of 250 random sorts of samples using BioDiversityProfessional Beta 1 (McAleece 1997) (> 10 samples), or by calculating averages of all possible combinations of samples (< 10 samples). Samples were grouped according to type of change. In addition, samples were grouped according to their compartment, as homogenisation resulting from large scale rewetting will manifest itself on that scale level.

To investigate changes in frequency of species occurring in bog pools, the change in frequency was calculated for each species for different types of change (1, 3a & 3c) as follows: freq\textsubscript{before} - freq\textsubscript{after} / total number of sites.

To investigate changes in species occurrence, each species was assigned to a status category (ranging from very scarce to very abundant), based on their frequency and abundance in the research area. Species were assigned twice, before measures took effect and after the execution of measures, using the same criteria (Table 1) and the difference (status change), expressed as the number of categories a species went up or down was calculated for all species found before measures took effect. A full list of the taxa found in this study and their status can be found in Verberk & Esselink (2006).

**RESULTS AND DISCUSSION**

At the scale of a single water body, average species richness increased (Fig. 2). Both type of change and compartment significantly explained the change in species richness, while the change in species diversity differed between compartments only (Table 2). The average species richness increased most in unchanged water bodies (type 1) and water bodies with increased ground water influence (type 2c and 3c) and in compartments 3 and 4. Most water bodies in these compartments had no, or only minor changes.

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**Table 1.** Criteria used to assign species to a status category.

<table>
<thead>
<tr>
<th>Status</th>
<th>Frequency (# sites)</th>
<th>Abundance (# individuals)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Absent</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Very scarce</td>
<td>1</td>
<td>1-2</td>
</tr>
<tr>
<td>Scarce</td>
<td>2-3</td>
<td>3-8</td>
</tr>
<tr>
<td>Fairly scarce</td>
<td>4-7</td>
<td>9-26</td>
</tr>
<tr>
<td>Fairly abundant</td>
<td>8-15</td>
<td>27-80</td>
</tr>
<tr>
<td>Abundant</td>
<td>16-31</td>
<td>81-242</td>
</tr>
<tr>
<td>Very abundant</td>
<td>≥32</td>
<td>≥243</td>
</tr>
</tbody>
</table>

CONSERVATION BIOLOGY
At a larger scale, viz. compartments and groups of water bodies with a similar type of change, cumulative species richness decreased in many cases, contrasting with the increase in average species richness per water body (Fig. 3). Impacted water bodies in rewetted parts where changes in water quality indicated a decrease in groundwater influence (type 2a en 3a) showed a decrease in cumulative species richness. In impacted bog pools where changes in water quality indicated an increase in groundwater influence (type 3c), the cumulative species richness increased. Rewetting of the raised bog compartments (1, 2 and 3)

![Figure 2. Species richness (± S.E.) per water body, averaged per type of change (upper) and per compartment (lower).](image-url)
Table 2. ANCOVA results.

<table>
<thead>
<tr>
<th></th>
<th>df</th>
<th>F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Number of species</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>corrected model</td>
<td>20</td>
<td>5.168</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>intercept</td>
<td>1</td>
<td>60.301</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>compartment * time</td>
<td>6</td>
<td>4.923</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>type of change * time</td>
<td>6</td>
<td>2.434</td>
<td>0.034</td>
</tr>
<tr>
<td>water type * time</td>
<td>7</td>
<td>0.878</td>
<td>0.529</td>
</tr>
<tr>
<td><strong>Shannon index</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>corrected model</td>
<td>20</td>
<td>2.831</td>
<td>0.001</td>
</tr>
<tr>
<td>intercept</td>
<td>1</td>
<td>150.57</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>compartment * time</td>
<td>6</td>
<td>2.474</td>
<td>0.032</td>
</tr>
<tr>
<td>type of change * time</td>
<td>6</td>
<td>1256</td>
<td>0.290</td>
</tr>
<tr>
<td>water type * time</td>
<td>7</td>
<td>1.578</td>
<td>0.157</td>
</tr>
</tbody>
</table>

Figure 3. Species accumulation curves for water bodies grouped according to type of change (upper) and compartment (lower). Open symbols indicate the sampling period before measures took effect, while filled symbols indicate the sampling period after the execution of measures.
decreased the cumulative species richness, except for compartment 3 where most water bodies had no or minor changes only.

How can this increase in average species richness per water body and decrease in cumulative species richness be explained? The changes caused by rewetting offer new opportunities for some species, while causing problems for others. Because the induced changes will be similar over a large area, the same species will be able to profit over a large area and – as a result – will become more frequent and abundant. At the scale of a single water body, more species can be gained than lost, especially when species disperse from rewetted areas to adjacent sites with minor changes, either because they have become abundant or in order to evade the changes. At the scale of compartments or the whole nature reserve, everywhere the same species are gained, but different species are lost, resulting in a decrease in cumulative species richness. This effect will be

![Figure 4. Changes of frequency for species in bog pools, subdivided by type of change.](image)

---: decrease in frequency >67%; --: decrease in frequency between 67% and 33%; -: decrease in frequency between 33% and 15%; -/+: change in frequency between ±15% and +15%; +: increase in frequency between 15% and 33%; ++: increase in frequency between 33% and 67%; +++ increase in frequency >67%.
stronger in water bodies impacted by rewetting measures (higher losses) and when water bodies are grouped per compartment (more homogenisation of environmental conditions and thus a higher similarity in species gained).

For bog pools, changes in species frequency differed between sites with an increased, decreased and unchanged influence of groundwater. In bog pools with no or minor changes, most species (66%) occurred in more or less the same frequency (Fig. 4). In impacted sites the frequency of only few species (20% and 24% for 3a and 3c, respectively) stayed more or less the same. In bog pools with a decrease in groundwater influence (type 3a) a number of species (38%) increased in frequency, but a larger number of species (42%) decreased in frequency, while in bog pools with an increased groundwater influence (3c), more species (49%) increased, including characteristic and rare species such as *Agabus congener* and *Limnephilus elegans*. Improving groundwater conditions promotes the habitat diversity and increases opportunities for the occurrence of characteristic and rare species.

Especially mobile and abundant species are expected to profit most from the changes (Verberk & Esselink 2006). This homogenisation of the invertebrate assemblages was also evident on the scale level of the entire reserve (Fig. 5). On average, abundant species increased, while scarce species decreased.

**Conclusion**

These results show that large scale retention of water to improve conditions for *Sphagnum* growth is not sufficient for restoration of the entire raised bog ecosystem. Swift rewetting can cause shock effects species cannot cope with and large-scaled rewetting leads to similar changes over a large area, resulting in a loss of variation between patches (loss of heterogeneity) and consequently leads to a loss of species. Many macroinvertebrates, including rare and characteristic

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*Figure 5.* Shift in species status after execution of measures. Species are classified according to their status before measures took effect. Therefore, species only found after the execution of measures (39 spp.) are not shown.
species, depend on small-scale variation within (Verberk et al. 2005) and between water bodies, in e.g. depth, surface size, vegetation structure, shading, permanence, and minerotrophic influence (Moller Pillot 2003; Van Duinen et al. 2003, 2004; Verberk & Esselink 2006; Verberk et al. 2006). Especially the minerotrophic influence of groundwater, naturally occurring in lagg zones and transitional mires, has decreased during the gradual process of degradation. Retention of rain water decreases this influence even further. Although the process of bog restoration will take much longer than the period studied here, this study shows that in the short term, both the survival of scarce aquatic invertebrates and preservation of suitable habitat conditions are in jeopardy.

Restoration measures should therefore aim at a gradual improvement of growth conditions for Sphagnum and increasing the heterogeneity of the landscape. Because influence of calcareous groundwater can also stimulate Sphagnum growth (Lamers et al. 1999), these goals can be reconciled when measures aim at improving the regional hydrology. This requires more attention to the landscape scale in bog restoration projects.

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REFERENCES


