Nutrient enrichment changes the nature of invertebrate food webs in raised bog pools

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Summary
Drainage and increased atmospheric nitrogen and sulphur deposition results in increased nutrient availability in naturally nutrient-poor bogs. To study if increased nutrient availability changes the bog food web, stable isotope ratios of carbon and nitrogen of basal food sources (living plants and dead organic matter) and invertebrates were compared between bog pools, differing in nutrient availability, in Estonia and the Netherlands. For part of the invertebrate community, trophic relations could not be inferred from measured basal food sources. One or more basal carbon sources with a low stable isotope ratio for carbon still need to be identified. This unidentified carbon source becomes less important with increasing nutrient availability.

Key index words: eutrophication, nutrients, fauna, invertebrates, food web

Introduction
Intact raised bogs are extremely nutrient-poor and bog plants have correspondingly low nutritional value. Due to atmospheric nitrogen and sulphur deposition nutrient availability has increased in Western European raised bog pools and a simultaneous change in the invertebrate species composition has been documented (Desrocher and Van Duinen, 2006; Van Duinen et al., 2006). SO4 can lead to an increased release of NH4 and PO4 from the peat substrate in bog pools (Lamers et al., 1998). Increased nutrient availability in raised bogs leads to a higher cover of vascular plants such as Molinia caerulea and Betula spp. and an elevated N-content of Sphagnum mosses (Lamers et al., 2000). As a result, both the input and nutritional value of dead organic material in bog pools increase. Additionally, algal growth rate and nutrient content are increased. These changes in quantity and quality of food sources at the start of the aquatic food web may underlie the observed changes in invertebrate species composition. This paper addresses the question whether the increased nutrient availability has caused changes in the importance of basal food sources that may have led to cascading effects through the invertebrate food web in bog pools.

Material and methods
Stable isotope ratios of carbon and nitrogen of basal food sources and aquatic invertebrates were compared between nine bog pools differing in nutrient availability. Three bog pools were sampled in Nigula bog, Southwest Estonia, between 9 and 23 September 2002. In the Netherlands, six peat cuttings and inundated peat extraction fields were sampled in five raised bog remnants in total between 7 October and 15 November 2002. At each site surface water and sediment pore water samples were collected for analysis of nutrient availability (Table 1). For further details about water quality analyses see Van Duinen et al. (2006).

At all sampling sites plants (filamentous algae, mosses and vascular plants) and aquatic macroinvertebrates were collected. Settled dead organic matter was collected from the peat bottom by means of a plankton net with mesh size 45 μm. Zooplankton was collected from the open water by means of this plankton net and light traps. Gut contents were not removed from invertebrates. The collected material was sorted, washed with demineralised water and kept in a fridge until identification. Identified material was dried for 24 hours at 70°C and subsequently ground, using liquid nitrogen. Carbon and nitrogen isotopic composition was determined. Average reproducibilities of duplo and triplo measurements were <0.2‰. Stable isotope data are presented as the relative difference between the ratios of the sample and the standards, using the following formula:

\[
\delta R = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000
\]

where R = 13C/12C or 15N/14N, \(\delta^{13}C\) or \(\delta^{15}N\) is the per mille (%) deviation of the sample from their isotope standards, that are PeeDee belemnite for \(\delta^{13}C\) and atmospheric N2 for \(\delta^{15}N\).
Results and Discussion

Different invertebrate species collected within the same bog pool differ in their $\delta^{13}C$, indicating differential use of carbon sources, and in their $\delta^{15}N$, indicating the presence of various trophic levels in the invertebrate community (Figure 1). For dead organic matter and plants, as well as most invertebrate species within the food web, inferred from their $\delta^{15}N$ corresponded with common ecological knowledge.

In food web studies generally an enrichment of 0 to 1‰ (less negative) for $\delta^{13}C$ between trophic levels is found (McCutchan et al., 2003). Only for the two most nutrient rich sites (Bargerveen and Mariapeel) all collected invertebrate species appeared to be similar or enriched in $\delta^{13}C$ compared to basal food sources (dead organic matter and living plants). In the three Estonian sites and the less nutrient-rich Dutch sites many invertebrates were depleted (more negative) in $\delta^{13}C$ compared to the analysed basal food sources. For example, in pool Nigula 1, $\delta^{13}C$ of dead organic matter and living plants ranged from -28.3 to -24.3‰, whereas $\delta^{13}C$ of invertebrates ranged from -34.8 to -24.2‰ (Fig. 1). Although consumers can be depleted in $\delta^{13}C$ relative to their food sources by more than 2‰ (McCutchan et al., 2003), the depletion was not consistent for all sampling sites. The difference between the average $\delta^{13}C$ of all basal food sources and the average $\delta^{13}C$ of all invertebrates (=average trophic shift) correlated strongly and positively to nutrient concentrations of surface water ($p < 0.025$) and sediment pore water ($p < 0.001$; Fig. 2).

For the nutrient poor bog pools still one or more important basal carbon sources with $\delta^{13}C < -30‰$ need to be identified. The still unidentified basal carbon sources become less important with increasing nutrient availability. In a study on lake zooplankton, Grey et al. (2000) concluded that the relative importance of allochthonous sources of organic carbon decreases with increasing lake

<table>
<thead>
<tr>
<th>Site</th>
<th>Surface water pH</th>
<th>o-PO4</th>
<th>NO$_3$+NH$_4$</th>
<th>Sediment pore water pH</th>
<th>o-PO4</th>
<th>NO$_3$+NH$_4$</th>
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<td></td>
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<tr>
<td>Nigula 1</td>
<td>4.2±0.3</td>
<td>0.2±0.1</td>
<td>13±14</td>
<td>4.9±0.2</td>
<td>0.2±0.1</td>
<td>5.4±4.0</td>
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<tr>
<td>Nigula 2</td>
<td>4.0±0.0</td>
<td>0.1±0.1</td>
<td>12±5.6</td>
<td>4.8±0.7</td>
<td>0.2±0.1</td>
<td>15±16</td>
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<tr>
<td>Nigula 3</td>
<td>3.9±0.1</td>
<td>0.3±0.0</td>
<td>11±9.0</td>
<td>4.5±0.2</td>
<td>0.2±0.1</td>
<td>21±14</td>
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<tr>
<td><strong>The Netherlands</strong></td>
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<td>0.8±0.4</td>
<td>14±12</td>
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<td>1.3±1.2</td>
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</tr>
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<td>Haaksbergerveen 2</td>
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<td>5.1±0.9</td>
<td>0.8±0.1</td>
<td>21±11</td>
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<td>Mariapeel</td>
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<td>20±16</td>
<td>4.5±0.5</td>
<td>82±102</td>
<td>213±219</td>
</tr>
</tbody>
</table>

Table 1. Average (± sd) pH and concentrations of o-PO$_4$ and NO$_3$+NH$_4$ (μmol/l) of surface water and sediment pore water at the nine sampling sites.

Figure 1. Scatter plot of $\delta^{15}N$ against $\delta^{13}C$ of dead organic matter, plants (vascular plants, mosses and filamentous algae) and aquatic invertebrates of the intact raised bog pool Nigula 1.
trophic. In the case of the pools sampled in Nigula bog, these allochthonous food sources could be pollen, seeds or leaves of *Betula* and *Pinus* trees, that are scattered in the surrounding bog, and terrestrial insects, for example ants and butterflies, falling and drowning in the pool. The δ13C of *Betula* leaves and terrestrial invertebrates collected here was > -29.6‰. Alternatively, in oligotrophic lakes in which phytoplankton production is limited, zooplankton diets are supported by planktonic heterotrophic and detritus via the microbial pathway (Hessen et al., 1990; Jones, 1992). Methanotrophic or chemoautotrophic bacteria are known to have a δ13C < -40‰ and are assimilated by invertebrates such as chironomid larvae (Kiyashko, 2004; Grey and Deines, 2006) and zooplankton (Taipale et al., 2007).

We suggest that only in the most nutrient enriched raised bog pools the quality of dead organic matter and/or the abundance and quality of algae are sufficient to support the whole invertebrate community. In the pristine or less nutrient enriched pools one or more basal carbon sources with δ13C < -30‰ are more important. Thus, nutrient enrichment in bog pools changes the importance of basal carbon sources in the invertebrate food webs.

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**References**


Preparing the ground

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Summary

The concentration of raised peat bogs across the centre of Ireland is often attributed simply to the poorly
drained nature of the Shannon basin and the former occurrence of a broad interconnecting network of lakes
across the postglacial landscape. This describes the conditions that obtained, but not the cause. The nature of
deglaciation, the disposition of the retreating ice sheets relative to one another and the isostatic lowering of the
land surface were critical factors in determining the conditions that lead to the rapid growth of basin peat in
the central midlands. Fundamental to this was the way in which the ice sheet, which had been composed of a
number of coalescing ice domes broke up into its constituent parts while the domes retreated back to their
centres of dispersion.

Key index words: Irish midlands, deglaciation, glaciolacustrine, postglacial, isostacy

Introduction

The bogs of the midlands of Ireland are founded almost
exclusively on late Quaternary glacial, glaciofluvial, and
most particularly, glaciolacustrine deposits. Commonly,
the raised bogs are easily seen to be separated by ridges or
hills of relatively well-drained mineral soil: coarse esker
gravels, fans of well-bedded sands and gravels, and a
mixture of low permeability and medium permeability
glacial tills. The immediately sub-peat substrate in the peat
basins was until recently poorly known and very little
understood. This uncertainty as to the sub-peat geology
raised the obvious question as to the influence of this
substrate on the evolution of the basin peats that charac-
terise the midlands. This presentation attempts to
summarise the current understanding of the sub-peat
Quaternary geology of the midlands and to consider the
possible influence of isostatic depression on the evolution
of the raised bogs of the midlands of Ireland. It focuses on
work carried out in investigating the raised bogs at Clara
and Raheenmore in County Offaly (see Schouten, 2002),
on investigations as to the characterisation of the eskers of
the midlands (see Warren and Ashley, 1994) and on
ongoing geological mapping by the Geological Survey of
Ireland.

Glaciation and deglaciation of the Irish
midlands

There is unequivocal geological evidence for no more than
two Pleistocene glacial events in Ireland, and in by far the
greater part of the country we see evidence of no more than
one, the most recent, termed the Fenitian Glaciation
(Warren, 1985). The important glacial features (the eskers,
subaqueous fans, deltas and drumlins) that, together with
the raised peat bogs, dominate the landscape of the
midlands of Ireland all relate to this final glaciation, and
most of these, in particular the esker complexes, to the final
acts of deposition during deglaciation (Warren and Ashley,
1994).

The overall pattern of the glaciation of Ireland has been
understood in outline since Maxwell Close (1867) carried out
his seminal work more than 140 years ago. It is unfortunate
that this work was very little understood at the time, and that
a model of glaciation later emerged, largely influenced by
Charlesworth (1928), which postulated a simple ice sheet that
extended from north to south and receded again from south
to north, came to be established as the working model of our
understanding of the events of the last glaciation for a period
of more than fifty years (e.g. Synge, 1970). More recently a
model that relates directly to the available evidence for ice
movement and to the deglacial processes has been developed
(Warren, 1992). This is very close to the model presented by
Close and has been rigorously tested in the midlands with
regard to the pattern of deglaciation and to esker genesis (see
Warren and Ashley, 1994). According to this model the Irish
ice sheet was composed of a number of discrete ice domes,
initially separate ice sheets, which coalesced to form a single
body, but retained a flow pattern driven by the operation of
the snow collection areas as individual centres of ice dispersal
(Fig. 1). Thus the important elements of the Irish ice sheet
were the Northern Dome, the Central Dome, the Southern
Dome and the Irish Sea ice lobe.

During deglaciation, all of these bodies separated one
from the other as they shrank back to their respective
centres of dispersion. As the Northern and Central Domes
separated, they did so initially along the east to west line of
suture, and the area between the two separating domes was
flooded by the emerging meltwater. The Shannon/Boyne
interfluve held up this lake at its eastern end and controlled
its depth. All of the deglacial sediments, the extensive esker
systems and the great fans and deltas, of the central
midlands were deposited into this lake. These are the readily