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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). SO_4 can lead to an increased release of NH_4 and PO_4 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:

$$\delta R = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$. $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ is the per mille (‰) deviation of the sample from their isotope standards, that are Pee Dee belemnite for $\delta^{13}\text{C}$ and atmospheric N_2 for $\delta^{15}\text{N}$.



Table 1. Average (\pm sd) pH and concentrations of o-PO₄ and NO₃+NH₄ (μ mol/l) of surface water and sediment pore water at the nine sampling sites.

Site	Surface water			Sediment pore water		
	pH	o-PO ₄	NO ₃ +NH ₄	pH	o-PO ₄	NO ₃ +NH ₄
<i>Estonia</i>						
Nigula 1	4.2 \pm 0.3	0.2 \pm 0.1	13 \pm 14	4.9 \pm 0.2	0.2 \pm 0.1	5.4 \pm 4.0
Nigula 2	4.0 \pm 0.0	0.1 \pm 0.1	12 \pm 5.6	4.8 \pm 0.7	0.2 \pm 0.1	15 \pm 16
Nigula 3	3.9 \pm 0.1	0.3 \pm 0.0	11 \pm 9.0	4.5 \pm 0.2	0.2 \pm 0.1	21 \pm 14
<i>The Netherlands</i>						
Haaksbergerveen 1	4.2 \pm 0.2	0.8 \pm 0.4	14 \pm 12	4.8 \pm 0.5	1.3 \pm 1.2	46 \pm 21
Haaksbergerveen 2	4.2 \pm 0.1	2.2 \pm 2.8	13 \pm 7.4	5.5 \pm 0.5	1.7 \pm 0.5	40 \pm 14
Korenburgerveen	3.7 \pm 0.1	0.9 \pm 0.2	11 \pm 4.1	5.1 \pm 0.9	0.8 \pm 0.1	21 \pm 11
Reigerplas	4.2 \pm 0.5	0.4 \pm 0.3	8.3 \pm 2.8	5.0 \pm 0.0	3.2 \pm 2.3	110 \pm 131
Mariapeel	4.0 \pm 0.1	3.4 \pm 17	23 \pm 21	5.0 \pm 0.4	18 \pm 19	201 \pm 117
Bargerveen	3.8 \pm 0.1	5.6 \pm 8.2	20 \pm 16	4.5 \pm 0.5	82 \pm 102	213 \pm 219

Results and Discussion

Different invertebrate species collected within the same bog pool differ in their $\delta^{13}\text{C}$, indicating differential use of carbon sources, and in their $\delta^{15}\text{N}$, 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 trophic levels in the food web inferred from their $\delta^{15}\text{N}$ corresponded with common ecological knowledge.

In food web studies generally an enrichment of 0 to 1‰ (less negative) for $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ compared to the analysed basal

food sources. For example, in pool Nigula 1, $\delta^{13}\text{C}$ of dead organic matter and living plants ranged from -28.3 to -24.3‰, whereas $\delta^{13}\text{C}$ of invertebrates ranged from -34.8 to -24.2‰ (Fig. 1). Although consumers can be depleted in $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ of all basal food sources and the average $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C} < -30$ ‰ 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

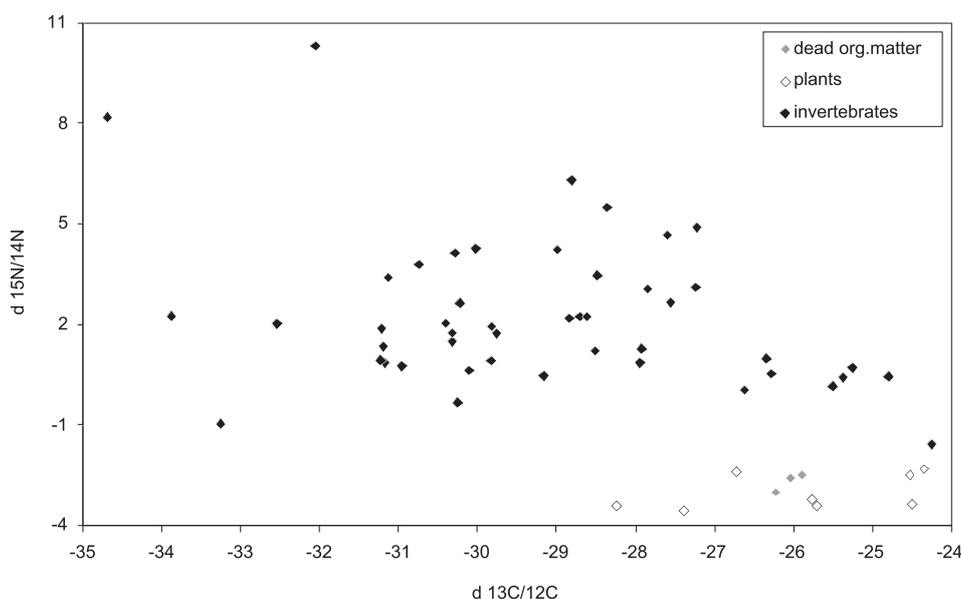


Figure 1. Scatter plot of $\delta^{15}\text{N}$ against $\delta^{13}\text{C}$ of dead organic matter, plants (vascular plants, mosses and filamentous algae) and aquatic invertebrates of the intact raised bog pool Nigula 1.

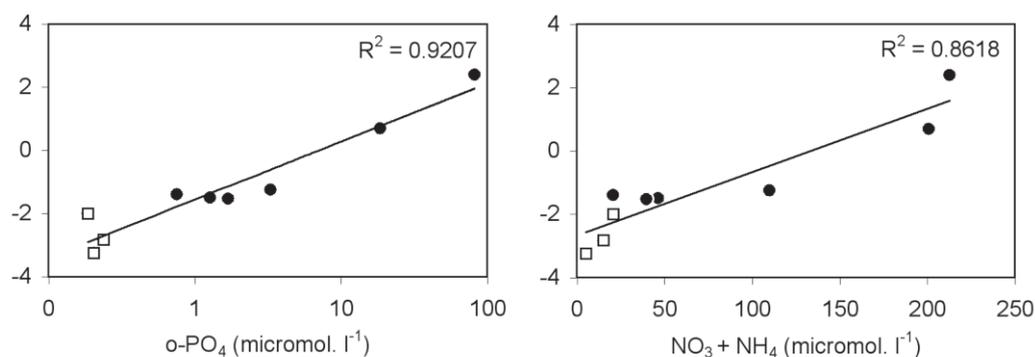


Figure 2. Relationship between the o-PO_4 and $\text{NO}_3 + \text{NH}_4$ concentrations in sediment pore water and the average trophic shift for the nine sampling sites. Open squares for Estonian sites and filled circles for Dutch sites.

trophy. 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 $\delta^{13}\text{C}$ of *Betula* leaves and terrestrial invertebrates collected here was $> -29,6\text{‰}$. Alternatively, in oligotrophic lakes in which phytoplankton production is limited, zooplankton diets are supported by planktonic heterotrophs and detritus via the microbial pathway (Hessen *et al.*, 1990; Jones, 1992). Methanotrophic or chemoautotrophic bacteria are known to have a $\delta^{13}\text{C} < -40\text{‰}$ 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 $\delta^{13}\text{C} < -30\text{‰}$ 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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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, isostasy

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 characterise 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 interfluvium 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