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 \( R = ^{13}\text{C} / ^{12}\text{C} \text{ or } ^{15}\text{N} / ^{14}\text{N} \), \( \delta^{13}\text{C} \text{ or } \delta^{15}\text{N} \) is the per mille (‰) deviation of the sample from their isotope standards, that are PeeDee belemnite for \( \delta^{13}\text{C} \text{ and atmospheric } \text{N}_2 \text{ for } \delta^{15}\text{N} \).
Results and Discussion

Different invertebrate species collected within the same bog pool differ in their δ13C, indicating differential use of carbon sources, and in their δ15N, 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 δ15N corresponded with common ecological knowledge.

In food web studies generally an enrichment of 0 to 1‰ (less negative) for δ13C 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 δ13C 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 δ13C compared to the analysed basal food sources. For example, in pool Nigula 1, δ13C of dead organic matter and living plants ranged from -28.3 to -24.3‰, whereas δ13C of invertebrates ranged from -34.8 to -24.2‰ (Fig. 1). Although consumers can be depleted in δ13C 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 δ13C of all basal food sources and the average δ13C 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 δ13C < -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 food sources.
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 $\delta^{13}C$ of *Betula* leaves and terrestrial invertebrates collected here was $>-29.6\%_o$. 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 $\delta^{13}C < -40\%o$ 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 $\delta^{13}C < -30\%o$ 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**


