The importance of gradual changes and landscape heterogeneity for aquatic macroinvertebrate diversity in mire restoration management

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Relict populations in degraded bogs

Raised bogs are threatened ecosystems, especially in Western Europe (Joosten & Clarke 2002) and temperate North America (Poulin & Pellerin 2001), due to drainage, afforestation, peat extraction and increased atmospheric nitrogen deposition. As *Sphagnum* growth is a necessary prerequisite for the restoration of peat-accumulating raised bogs, restoration measures in degraded bogs mainly focus on creating suitable hydrological conditions for re-colonization and growth of *Sphagnum* by blocking drainage ditches and building dams to retain rainwater and decrease fluctuations of the water table (e.g., Rochefort *et al.* 2003, Smolders *et al*. 2003, Vasander *et al.* 2003). Only in a few cases do measures focus on restoring suitable conditions for the animal species that depend on bog habitats. Recovery of characteristic fauna is often assumed to follow automatically in the course of time. Although animals, especially invertebrates, make up an important part of the total species diversity, relatively little attention has been paid to how restoration measures affect the fauna, both in raised bog remnants and other ecosystems (Longcore 2003, Van Duinen *et al.* 2003, Desrochers & Van Duinen 2006, Van Kleef *et al.* 2006).

To study whether raised bog restoration measures rehabilitate faunal diversity, we studied the aquatic invertebrate assemblages in degraded bog remnants in the Netherlands. Study sites were divided into two groups: 1) 27 sampling sites in bog remnants that where rewetted 1–29 years ago (rewetted sites), and 2) 20 sampling sites in non-rewetted Dutch bog remnants (remnant sites). These remnant sites were water bodies in bog remnants that had not been subject to large-scale restoration measures; rather, with the cessation of bog use (which was practised prior to 1950), the remnant sites continued to remain in forms such as abandoned water-filled hand peat cuttings and trenches used in buckwheat agriculture. The comparison between the rewetted and non-rewetted sites showed that the cumulative species richness for

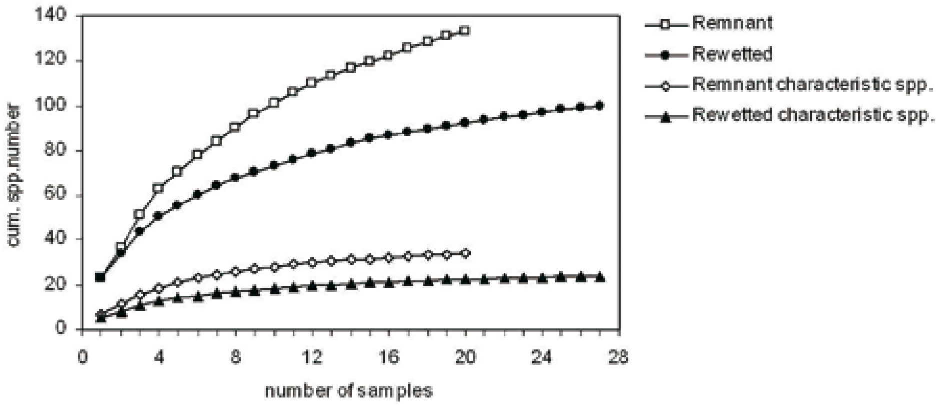

Figure 1. Cumulative species richness curves for all species and for characteristic species of macroinvertebrates in rewetted and (non-rewetted) remnant sampling sites in Dutch bog reserves. The curves are composed of averages of 250 random sorts of the sampling sites, with all samples taken at one sampling site pooled (modified from: Van Duinen et al. 2003).

macroinvertebrates (like water beetles and larvae of dragonflies or midges) was lower at rewetted sites than at non-rewetted sites, both for total species richness and for characteristic species (Fig. 1; Van Duinen *et al.* 2003). In this study species were classified as characteristic of raised bogs if they were listed in literature as acidophilous, acidobiontic, tyrphophilous, tyrphobiontic or typical of raised bogs. This indicates that degraded bog remnants, with little or no botanical value, can still harbour many animal species, including characteristic and rare species.

Effects of rewetting measures

Since most restoration projects do not include a monitoring programme for invertebrates, their effect on the fauna, whether positive or negative, is generally unknown. Our comparative study between the rewetted and remnant (non-rewetted) sites showed considerable differences in the macroinvertebrate species assemblage (Fig. 2). Surface water quality and vegetation composition could not explain the observed differences in aquatic macroinvertebrate assemblages between these two groups of sites (Van Duinen *et al.* 2003). In addition, the variation in species composition between sites (Beta diversity) was much lower in rewetted sites, suggesting that rewetting measures have a homogenizing effect.

This comparative research provides a strong indication that there may be risks involved in the restoration of remnants, where rare and characteristic species are still present. This indication was confirmed in a study where aquatic invertebrates were studied in the *same* peatland area before and after measures took effect (Verberk *et al.* 2006a; Verberk 2008). These risks are twofold: 1) *rapid* changes causing a disturbance (shock effects) that species cannot cope with; and 2) *similar* changes, but on a large-scale, leading to a loss of variation between patches within one peatland (loss of heterogeneity), and consequently to a loss of species. In a subsequent study, we showed habitat heterogeneity to be a driver of mire biodiversity (Verberk *et al.* 2006b, Verberk 2008). These risks are faced particularly by characteristic species because many of these species occur either in low densities, or very locally in just a few sites, or both (thus contributing to the need to take restoration measures focussing on both flora and fauna), and because these species usually depend, within a peatland, on patches with specific characteristics.

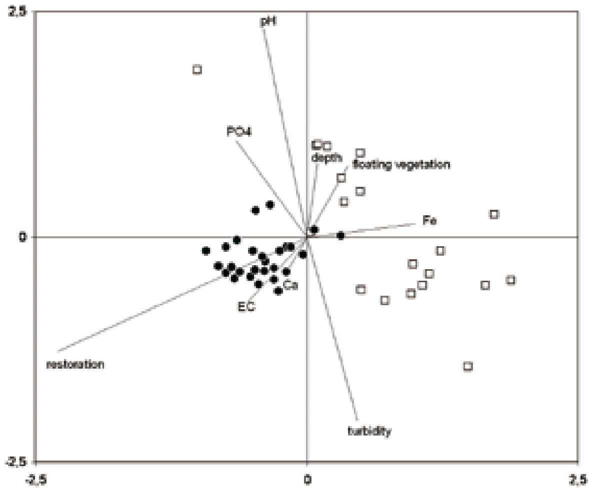

Figure 2. Correspondence Analysis plot of sampling sites based on presence/absence data of macroinvertebrate species. Significant environmental variables of surface water quality and vegetation are shown as lines. Filled circles represent rewetted sites, and open squares represent (non-rewetted) remnant sites in Dutch bog reserves (from: Van Duinen et al. 2003).

Persistence and re-colonization

In order to inhabit restored areas, species either have to persist in the area during the process of degradation and restoration, or they have to re-colonize the restored area from source populations. Concerning persistence, aquatic macroinvertebrate species, which are characteristic for raised bogs, usually have slow growth and high tolerance to drought and acidity. Due to their high tolerance, a number of species have been able to persist in the degraded bog remnants by surviving the slow process of degradation. However, many of these bog characteristic species have proved to be unable to cope with the rewetting of sites, most likely because the process of rewetting is much more rapid ("shocking") than the process of degradation. Other than this, rewetting tends to be large-scale and has the effect of lowering habitat diversity.

Moreover, in a study of natural and man-made bog pools in Canada, Mazerolle *et al.* (2006) concluded that some aquatic invertebrate species, including bog-associated species, readily colonize man-made bog pools created in a raised bog that had been mined for peat and where no aquatic invertebrates could have persisted. This conclusion is apparently valid for vagile aquatic beetle species of the genera *Acilius, Colymbetes, Dytiscus* and others found in the man-made bog pools in Canada, but probably not for more sedentary aquatic invertebrates, such as smaller water beetles, caddisflies, damselflies and aquatic oligochaetes (Van Duinen *et al.* 2007). Re-colonization by these species is thought to be low, as many species that are adapted to life in the non-dynamic bog ecosystem are incapable or not inclined to disperse over long distances. For example some beetles have reduced flight muscles or non-functional wings, having established their current distribution in historic times when more marshland existed (Jackson 1955).

Due to cultivation and habitat deterioration, the distance between remaining bog habitats has increased. This may have reduced colonization rates of bog-associated macroinvertebrates even further. In our comparative study, many rare and characteristic species were still absent in rewetted sites after 30 years, even though source populations were present nearby, sometimes even in the same bog remnant. This may be attributed to the above mentioned low dispersal capacity of characteristic species, or, more alarmingly, to an incomplete restoration of the conditions needed by these species.

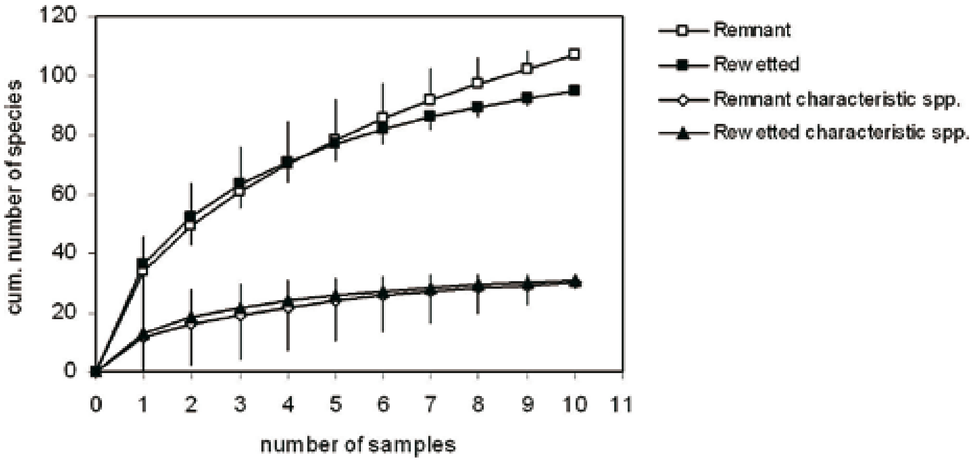

Figure 3. Cumulative species richness curves (± standard deviation) for all species and for characteristic species of microinvertebrates sampled in rewetted and (non-rewetted) remnant sampling sites in Dutch bog reserves. The curves are composed of averages of 250 random sorts of the sampling sites, with all samples taken at one sampling site pooled (from: Van Duinen et al. 2006).

In contrast to aquatic macroinvertebrates, species assemblage and species richness of micro-crustaceans and rotifers (including bog-associated species) did not differ between rewetted and non-rewetted sites in Dutch bog remnants (Fig. 3; Van Duinen *et al.* 2006). Unlike that of many aquatic macroinvertebrates, the lifecycle of these microinvertebrates does not include different life stages with different habitat demands; furthermore, their development time is generally shorter. Therefore, microinvertebrates may have less strict demands on their environment regarding, e.g. vegetation structure and the combination of habitat elements (heterogeneity). In addition, the high (passive) dispersal rate of micro-crustaceans and rotifers (easy dispersal by wind and animal vectors [Cáceres & Soluk 2002; Cohen & Shurin 2003]), may explain this difference in the response of macroinvertebrates and microinvertebrates.

Importance of landscape heterogeneity

Intact bog landscapes have a high landscape heterogeneity with bog margins, transitional mires and lagg zones between the raised bog centre (mire expanse) and the surrounding mineral soil (Wheeler & Proctor 2000; Schouten 2002). Even within the raised bog centre, there is much variation between bog pools in terms of size and depth, vegetation structure, water flow and nutrient availability (Smits *et al.* 2002). Our study on aquatic macroinvertebrates in the Estonian raised bog system Nigula showed that these differences, both within the landscape and within the raised bog centre, were exploited by the species present. Characteristic bog species did not occur just anywhere in the bog, but showed distinct distribution patterns. Certain characteristic species preferred locations with either lower or higher concentrations of nutrients and minerals (Smits *et al.* 2002). Minerotrophic, hydrologically stable transitions supported many characteristic species (Fig. 4). A study in a Dutch degraded bog remnant showed that several characteristic species selectively reproduced in temporary pools and others in permanent pools (Van Duinen *et al.* 2004). Even though the average number of species per water body was lower in Estonia than in the Dutch bog remnants, the Estonian species accumulation curve was more steep than the curve for rewetted sites, indicating a higher β-diversity (heterogeneity) in intact raised bog systems (Van Duinen *et al.* 2002).

Figure 4. Female Northern emerald (*Somatochlora arctica*) just after ecdysis. For its larval development (which can take up to 5 years), this species typically selects very shallow puddles, with a slight water flow, which guarantees stable moisture conditions. Adults prefer open areas surrounded by trees. These reproduction waters are usually situated at bog margins within transitional mires (photo: W.C.E.P. Verberk).

Implications for conservation and restoration

The conservation of aquatic macroinvertebrates requires the avoidance of both temporary and permanent loss of water types or rapid shifts in the spatial configuration (also emphasised in Van Duinen *et al.* 2003). In nature reserves of high ecological value, a first priority of restoration management is the conservation of relict populations of characteristic species and landscape heterogeneity. A second priority is the strengthening of landscape heterogeneity by improving the quality of the various parts of the landscape (raised bog centre, lagg zone, transitional mire) and their transitions. Improving growing conditions for *Sphagnum* species is but a single goal, albeit important in the *long term* for restoring the acrotelm layer, and thereby, the internal hydrology of raised bogs. In the *short term*, conserving present nature values and improving their situation is important, particularly given the low re-colonization observed. 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. These management goals can be achieved by taking measures outside the reserve, for example, reducing drainage (filling in ditches) and increasing infiltration (by logging trees). Should internal measures still be necessary, changes resulting from restoration measures should be slow and reversible, allowing species to gradually redistribute in response to the changes (Van Duinen *et al.* 2004). In addition, phased implementation of the measures, i.e. changing only small parts at a time, may allow local populations to recover from disturbance or re-colonize from adjacent unchanged locations. In sum, restoration measures should be directed at *gradually* improving growth conditions for *Sphagnum* and increasing the heterogeneity of the landscape, within the raised bog centre as well as transitions to the surrounding mineral soil (or agricultural or forested surroundings). This requires more attention to the landscape scale in bog restoration projects.

Tailor-made designs

Bog remnants differ in their geomorphological setting, remnant area and peat extraction history, therefore requiring tailor-made designs. Some significant questions to consider are: 1) what baseline inventories are necessary to assess the present species diversity, key processes in ecosystem functioning and factors limiting perspectives for restoration? 2) how can information from the different disciplines (hydrology, biogeochemistry, vegetation and animal ecology) be integrated for the optimal restoration strategy to be performed in a specific project area? 3) how can monitoring and interpreting the response of the species to restoration measures be used as a tool for "fine-tuning" the measures? Within the framework of the LIFE Nature Co-op project, "Dissemination of ecological knowledge and practical experiences for sound planning and management in raised bogs and sea dunes", two workshops were organised to facilitate international exchange of expertise to help with optimizing nature conservation and restoration measures. Based on common sense and experience, the PROMME approach was adopted by the participants of the workshops as a useful framework for the set up of restoration projects. PROMME is meant to check for pitfalls in the restoration process. This decision support system is freely available on the LIFE Co-op project website, www.barger.science.ru.nl/life, and further described and illustrated in Brouwer et al. (2005).

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