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

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Abstract
Raised bog 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.
To assess the effects of restoration measures on aquatic invertebrates, a comparative study was carried out between rewetted and non-rewetted raised bog remnants in the Netherlands and Estonian intact raised bogs as a reference. This study showed that degraded bog remnants may still harbour relic populations of rare and characteristic aquatic macroinvertebrates. The comparative study indicated that large scale rewetting measures may jeopardize the persistence of these relic populations, by causing (1) *rapid* changes (shock effects) species are unable to cope with, and (2) *similar* changes over a large scale leading to a loss of variation between patches (loss of heterogeneity) and consequently to a loss of species.
As recolonisation may be low, especially for the characteristic species, emphasis must be put on the conservation of existing nature values. Restoration measures should therefore aim at both a *gradual* improvement of growth conditions for *Sphagnum* and increasing the heterogeneity of the landscape. The study in intact raised bogs in Estonia show that minerotrophic transitions harbour many characteristic species. Because influence of calcareous groundwater can also stimulate *Sphagnum* growth, 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.

Relic 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 raised bog ecosystems, restoration measures in degraded bogs focus on creating suitable hydrological conditions for re-colonisation and growth of *Sphagnum* by blocking drainage ditches and building dams to retain rain water and decrease fluctuations of the water table (e.g., Rochefort *et al.* 2003, Smolders *et al.* 2003, Vasander *et al.* 2003). Recovery of characteristic fauna is often assumed to follow automatically in course of time. Although animals, and 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 (Longcore 2003, Van Duinen *et al.* 2003, Desrochers & Van Duinen 2006, Van Kleef *et al.* 2006).
To study whether raised bog restoration measures rehabilitate fauna diversity, we studied the aquatic invertebrate assemblages in degraded bog remnants in the Netherlands. Study sites were divided in two groups: (1) sites in bog remnants that where rewetted 1 to 29 years ago (rewetted sites) and (2) 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, but remained after ending the former use of bogs before 1950, e.g. abandoned water-filled hand peat cuttings and trenches used in buckwheat culture. The

comparison between the rewetted and non-rewetted Dutch sites showed that the cumulative species richness was lower at rewetted sites than at non-rewetted sites, both for characteristic species and total species richness (Figure 1; Van Duinen *et al.* 2003). 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 (Figure 2). Surface water quality and vegetation composition could not explain the observed differences in aquatic macroinvertebrate assemblages between these two groups (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 were aquatic invertebrates were studied in the *same* area before and after measures took effect (Verberk *et al*. 2006a). These risks are twofold: (1) *rapid* changes causing a disturbance (shock effects) species cannot cope with, and (2) *similar* changes over a large scale leading to a loss of variation between patches (loss of heterogeneity) and consequently to a loss of species. In a subsequent study, we showed habitat heterogeneity to be a driver of bog biodiversity (Verberk *et al.* 2006b). 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.

Recolonisation

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 recolonise the restored area from source populations. Mazerolle *et al.* (2006) concluded that some aquatic invertebrate species, including bog-associated species, readily colonise man-made bog pools created in a Canadian 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).

Aquatic macroinvertebrate species which are characteristic for raised bogs usually have slow growth and high tolerances to drought and acidity. Due to their high tolerance they have been able to persist in the degraded bog remnants by surviving the slow process of degradation. However, many of these bog characteristic species proved to be unable to cope with rewetting of the sites, most likely because the process of rewetting is much more rapid, large scaled and lowers habitat diversity.

Recolonisation is thought to be low, as many characteristic species 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). The distance between remaining bog habitats has increased. This may have reduced colonisation 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 alarming- to an incomplete restoration of the conditions needed by these species.

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 (Figure 3; Van Duinen *et al.* 2006). As microinvertebrates have a less complex lifecycle, they may have less strict demands on their environment (regarding e.g. vegetation structure, combination of habitat elements). In addition, 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 transitional mire and lagg zones (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 nutrient concentrations (Smits *et al.* 2002). Minerotrophic, hydrologically stable transitions supported many characteristic species (Figure 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).

Implications for conservation and restoration

The conservation of aquatic macroinvertebrates requires that a temporary or permanent loss of water types or rapid shifts in the spatial configuration is avoided (as was also emphasised by Van Duinen *et al.* 2003). In nature reserves of high ecological value, a first priority of restoration management is the conservation of relic populations of characteristic species and the landscape heterogeneity. A second priority is the strengthening of the 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 on the *long term* for restoring the acrotelm layer and thereby the internal hydrology. On the *short term*, conservation of the present nature values and improving their situation is important, which is further emphasized by the low recolonisation 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 by 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, changing only small parts at a time may allow local populations to recover from disturbance or recolonise from adjacent unchanged locations. In conclusion, restoration measures should therefore aim at a *gradual* improvement of growth conditions for *Sphagnum* and increasing the heterogeneity of the landscape. This requires more attention to the landscape scale in bog restoration projects.

Tailor-made designs

Bog remnants differ in their geomorphological setting, remnant area, peat extraction history, and therefore require tailor-made designs. What baseline inventories are necessary to assess the present species diversity, key processes in ecosystem functioning and factors limiting perspectives for restoration? How can information from the different disciplines (hydrology, biogeochemistry, vegetation and animal ecology) be integrated for a specific project area to arrive at the optimal restoration strategy? How can monitoring and interpreting the response of the species to restoration measures be used as a tool to determine the 'fine-tuning' of measures? In 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 optimising 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 website of the LIFE Co-op project: www.barger.science.ru.nl/life and further described and illustrated by Brouwer *et al.* (2005).

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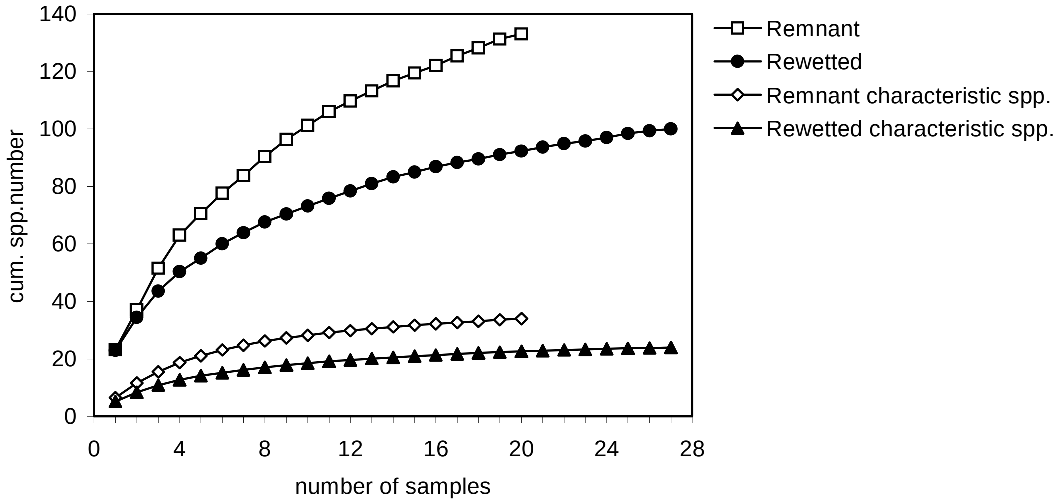

Figure 1. Cumulative species richness curves for all species and for characteristic species of macroinvertebrates in rewetted and remnant (not rewetted) sites in Dutch bog reserves. The curves are composed of averages of 250 random sorts of the sampling sites (Modified from: Van Duinen *et al.* 2003).

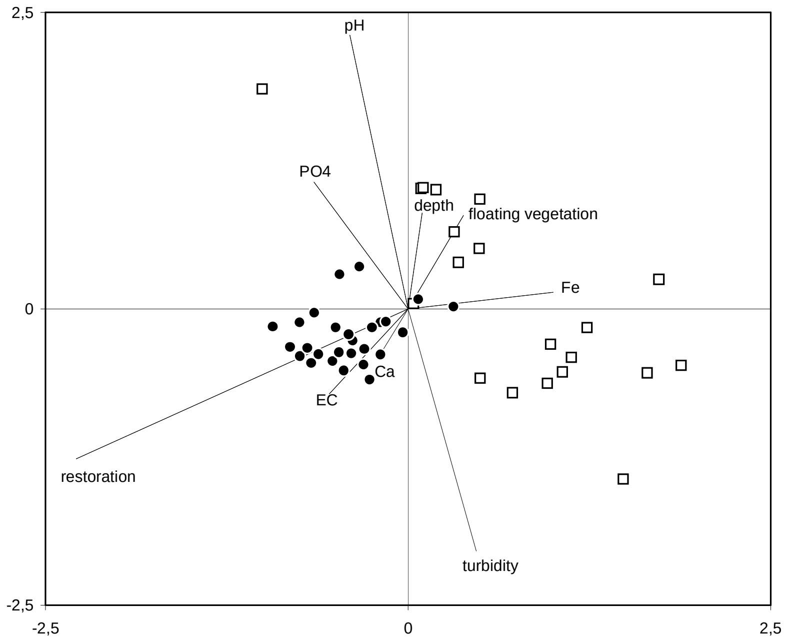

Figure 2. Correspondence Analysis plot of sampling sites based on presence/absence data of macroinvertebrate species. Significant environmental variables of surface water quality and vegetation are shown as lines. Filled circles represent rewetted sites and open squares represent (non-rewetted) remnant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

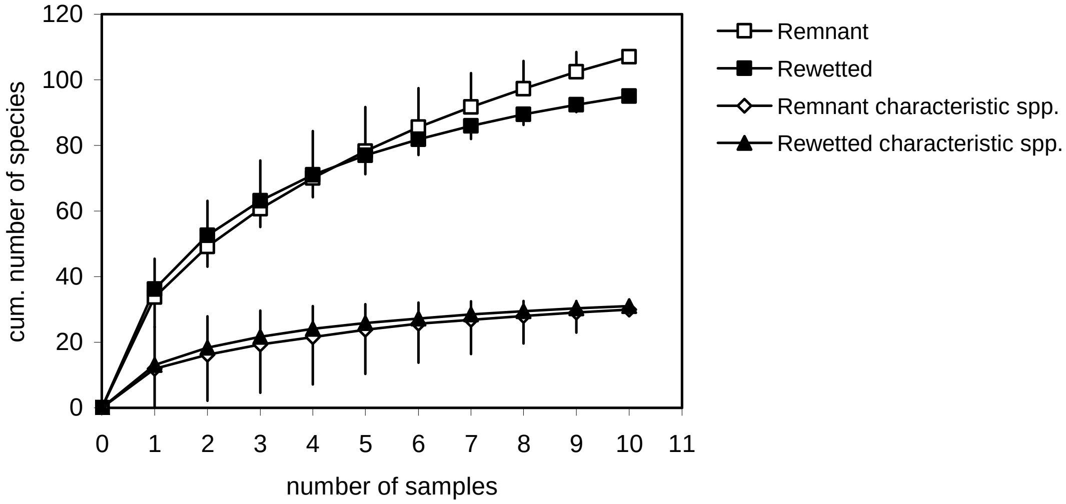

Figure 3. Cumulative species richness curves (± standard deviation) for all species and for characteristic microinvertebrate species sampled in rewetted and remnant sites in Dutch bog reserves. The curves are composed of averages of 250 random sorts of the sampling sites (From: Van Duinen *et al.* 2006).

Figure 4. Female of the 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, resulting in stable moisture conditions. Adults prefer open areas surrounded by trees. These reproduction waters are usually situated at the edges of the bog centre within transitional mires (Photo: W.C.E.P. Verberk).