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Importance of landscape heterogeneity for the conservation of aquatic macroinvertebrate diversity in bog landscapes

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Summary

Heterogeneous landscapes are biodiversity 'hotspots'. Degradation resulting from acidification, desiccation and eutrophication not only decreases habitat quality, but also causes heterogeneity to decline. While restoration measures aim at restoring habitat quality, they can further reduce heterogeneity when they affect large parts of an area (large scale) or cause disturbance (high intensity). Successful restoration of biological diversity therefore requires knowledge of the mechanisms underlying the relation between landscape heterogeneity and species diversity. This paper addresses two questions:

(1) Do bog pools in a heterogeneous landscape harbour more aquatic macroinvertebrate species than those located in more homogeneous landscapes?
(2) Is distance between water bodies an important factor determining species composition?

To answer the first question, aquatic macroinvertebrate assemblages in bog pools with a similar water chemistry range were studied in bog remnants differing in landscape heterogeneity. The most heterogeneous remnant (Korenburgerveen) had

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the highest scores on all diversity indices, indicating that bog pools situated in a heterogeneous landscape have a higher diversity than those located in more homogeneous landscapes.

To answer the second question, the most heterogeneous remnant was studied in greater detail. Adjacent water bodies were more similar in species composition than expected on the basis of differences in local environmental conditions. This indicates that not only environmental conditions, but also spatial configuration determines the species composition.

In conclusion, species diversity in heterogeneous landscapes (i.e. those with a combination of different parts) is greater than the total number of species that would be present if the individual parts were separated. Conservation and restoration strategies should not only focus on enlarging habitat areas and restoring a single habitat type, but also on conserving and strengthening landscape heterogeneity. We present some guidelines for improving habitat quality without causing heterogeneity to decline.

Introduction

A high environmental heterogeneity generally leads to a high species diversity. This relation has been described for various groups, such as birds (e.g. Cody, 1968; MacArthur & MacArthur, 1961), diatoms (e.g. Patrick, 1963) and aquatic macroinvertebrates (e.g. Harper, Mekotova, Hulme, White, & Hall, 1997; Heino, 2000; Ranta, 1985). The number of species is also known to increase with the size of the area (MacArthur & Wilson, 1967). However, when sampling a larger area, one inevitably samples greater heterogeneity, making it difficult to differentiate between effects of area size and heterogeneity. Knowledge of the factors controlling species diversity is important as macroinvertebrate species diversity is declining in Western Europe, due to habitat deterioration by acidification, desiccation and eutrophication (Heywood & Watson, 1995).

Unlike area size, landscape heterogeneity is difficult to quantify. A landscape is best described as a continuum without borders, but for practical reasons it is easier to distinguish individual patches (i.e. spatially explicit areas). Different patches can provide different functions for a particular species (reproduction, hibernation, foraging, etc.). A habitat is best defined, in relation to an organism, as the full complement of patches in a landscape that the organism needs to complete its life cycle. Landscape heterogeneity combines variations in patch quality (*habitat diversity*) and variations in size and distance between patches (*habitat configuration*). Because of their mobility, animals in particular are expected to be able to make use of the spatial heterogeneity of a landscape. Heterogeneous landscapes may therefore be characterised by high fauna diversity, including species not found in more homogeneous landscapes.

Environmental heterogeneity in natural landscapes is declining due to chronic large-scale processes of acidification, desiccation and eutrophication, resulting in reduced complexity (loss of habitat diversity and of gradual transitions between habitats) and fragmentation (deterioration of habitat configuration). Restoration and conservation measures based on a single discipline (e.g. hydrology, vegetation) do not make allowance for habitat diversity and habitat configuration at the scale level relevant to many animal species. These measures can result in a decline in landscape heterogeneity when they affect large parts of an area (large-scale measures) or cause disturbance (high-intensity measures). An example is the large-scale rewetting of peat bogs (Van Duinen et al., 2003). Therefore, successful restoration of biological diversity requires knowledge of the mechanisms underlying the relation between landscape heterogeneity and species diversity (Verberk & Esselink, 2003).

To investigate the effect of landscape heterogeneity on macroinvertebrate diversity, aquatic macroinvertebrate assemblages were compared between water bodies with similar environmental conditions (bog pools) but located in various Dutch bog remnants differing in landscape heterogeneity. We chose to study aquatic macroinvertebrates for several reasons. Restoration measures in bog remnants focus on restoring the hydrology by raising the surface water level and improving water quality. Water bodies can be regarded as individual habitat islands, which, like true islands, offer excellent opportunities to study fundamental ecological patterns and processes (Whittaker, 1998).

Furthermore, earlier studies have suggested that macroinvertebrates disperse in spring to reproduce, a process in which the spatial configuration of different water bodies may be important (Verberk et al., 2002). To investigate the effect of spatial configuration on species diversity, we studied the distribution of aquatic macroinvertebrates in one heterogeneous bog remnant in greater detail. This paper addresses two questions:

(1) Do bog pools in a heterogeneous landscape support more aquatic macroinvertebrate species than those located in more homogeneous landscapes?
(2) Is the distance between water bodies an important factor determining species composition?

Methods

Study area

Data were collected in seven raised bog remnants in The Netherlands from 1998 to 2001 (Fig. 1). All remnants sampled were degraded to a certain extent, as a result of peat cutting, drainage and atmospheric nitrogen deposition. In the natural configuration of a raised bog a distinct raised bog centre can be distinguished which is embedded in a landscape containing more minerotrophic parts and transitions between them. In the sampled remnants the natural configuration has been altered. The areas surrounding the raised bog remnants have been converted into agricultural lands, except at Dwingelerveld, where small raised bogs were situated in a dry, nutrient-poor forest. The most heterogeneous remnant was Korenburgerveen, where the raised bog centre was surrounded by more minerotrophic parts of the nature reserve, with several environmental gradients between the various parts (Fig. 3). Earlier studies have shown that Korenburgerveen offers a large variety of water types and a high diversity of water beetles (Verberk, Van Duinen, Peeters, & Esselink, 2001) and other animal species (Biologische Station Zwillbrock, 1995). As Korenburgerveen is relatively small (310 ha), these differences occur at relatively short distances, and as such, the Korenburgerveen can be characterised as the most heterogeneous of these seven bog landscapes. The raised bog parts of all remnant areas was characterised as acid, oligotrophic bog according to the classification by Wheeler and Proctor (2000), and were enriched by atmospheric nitrogen deposition and peat miner-
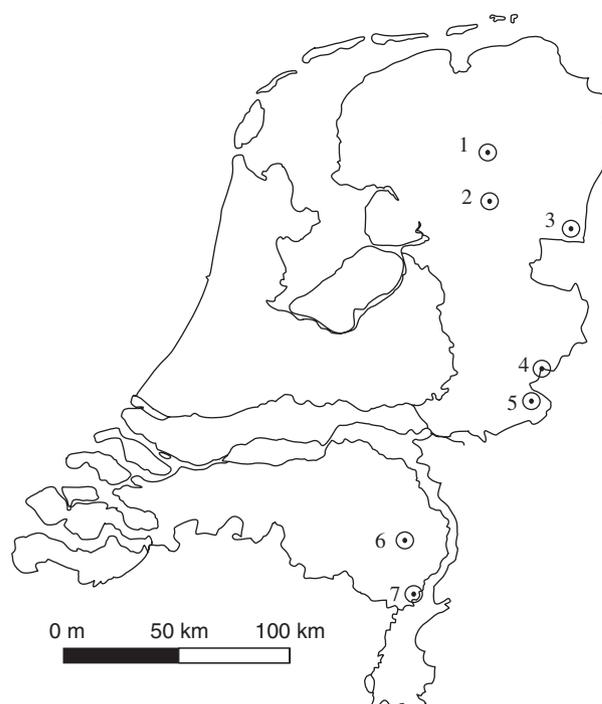
Figure 1. Locations of sampled raised bog areas in The Netherlands: (1) Fochteloërveen, (2) Dwingelerveld, (3) Bargerveen, (4) Haaksbergerveen, (5) Korenburgerveen, (6) Mariapeel, and (7) Tuspeel.

alisation, resulting in a dominance of *Molinia caerulea* and *Betula pubescens*.

Data collection

In the raised bog parts of the seven bog remnants, a total of 68 bog pools were sampled. Fifty pools were sampled in both spring and autumn, nine pools were sampled only in spring and nine pools were sampled only in autumn. The bog pools sampled differed in vegetation composition and structure, depth, size and bank profile. Sample sites were selected so as to include most of the variation present within the raised bog centre. At Korenburgerveen, additional water bodies were sampled, including minerotrophic, mesotrophic and eutrophic bodies to include both the variation present within the raised bog centre and that outside the raised bog centre. In total, 45 water bodies were sampled here. Thirty-seven water bodies were sampled in both spring and autumn, six water bodies were sampled only in spring and two water bodies were sampled only in autumn. The data collected were grouped into two different datasets to answer both research questions (Fig. 2). The first dataset comprised samples taken from

Question:	1. Heterogeneous more diverse?	2. Adjacent more similar?
Data:	68 Bog pools in 7 raised bog remnants	45 Waterbodies in Korenburgerveen

Calculations:	For each remnant:
	α diversity
	β diversity
	γ diversity
	N*
	Cumulative curves
		Calculate:
		
		$$\frac{\text{Dissimilarity in invertebrate species composition}}{\text{Dissimilarity in environmental conditions}}$$
		
		Between:
		(i) pairs of adjacent sites
		(ii) centroids of water types
		
		Needed:
		
		(i) Typology: 3 types, 8 subtypes
		
		(ii) Dissimilarity macroinvertebrate assemblage
		     CA on invertebrate abundance data
		     4 CA axes and Eigenvalues
		     $\sqrt{(\text{Axis 1})^2 \ ... \ (\text{Axis 4})^2}$
		
		(iii) Dissimilarity environmental conditions
		     Water chemistry → PCA (axis 1 & 2)
		     Vegetation → PCA (axis 1 & 2)
		     Physical aspects → PCA (axis 1 & 2)
		     Major environmental gradients
		     6 PCA Axes Lambda1 values
		
		     CCA on invertebrate abundance data
		     $\sqrt{(\text{Axis 1})^2 \ ... \ (\text{Axis 6})^2}$

Figure 2. Schematic overview of the data used and analyses performed for each research question (see text for more details).

seven bogs remnants distributed over The Netherlands, including a selection of samples taken from the bog remnant Korenburgerveen. The second dataset only included water bodies sampled in the bog remnant Korenburgerveen.

At all sampling sites, selected physical and chemical variables and vegetation composition were measured in the field. Water quality samples were analysed in the laboratory (for methods see van Duinen et al., 2003). For a full list of physical and chemical variables, see Verberk et al. (2001).

Macroinvertebrates were collected using a standard 30×20 cm pond net with a mesh size of 0.5 mm. Most samples consisted of a 1 m long sweep starting from the substrate and from more or less open water into denser vegetation near the shore. If the water body only included open water, one or more longer sweeps were taken to collect at least 100 macroinvertebrate individuals. In very dense *Sphagnum* vegetation, sweeps of 20–50 cm long were made to avoid the pond net becoming clogged with *Sphagnum*. As fauna abundance was generally high in this dense vegetation, most of these small samples contained over 100 individuals. At most sites, separate subsamples were taken to include different distinguishable microhabitats. All subsamples from a site were pooled before further analyses. Samples were transported to the laboratory and stored at 4 °C until analysis. The collected material was washed over three sieves with 2, 1, and 0.5 mm mesh sizes and sorted. Tricladida, Araneae, Crustacea, Cylindrotomidae, Odonata, Chaoboridae, Dixidae, Coleoptera (adults and larvae), Trichoptera, and Hemiptera (adults and nymphs) were identified to the lowest taxonomic level possible, which in most cases was the species level.

Typology

To test whether a pair of adjacent water bodies of a different water type share more species than the average for those water types, a typology was constructed. The water bodies sampled at Korenburgerveen could be classified into three types; bog

pools, mesotrophic waters and water bodies in wet forests (Table 1). The bog pools were mainly located on peat moss soils, and had low pH values. Three subtypes of bog pool were distinguished, differing in size, degree of shading and suscept-ibility to drying out, as well as in nutrient concentrations (o-PO_4^{3-}, NH_4^+ and NO_3^-). Water bodies in wet forests were heavily shaded and shallow. Two subtypes were distinguished, differing in pH and alkalinity as well as in nutrient concentrations. Mesotrophic water bodies were mainly located on podzol soils (except for strongly buffered mesotrophic pools) and water quality ranged from weakly buffered to highly buffered. Three subtypes of mesotrophic water bodies were distinguished, differing mainly in size, alkalinity and depth. To get an overview of the spatial configuration of the different water types, the environmental conditions of each water type were extrapolated using spatial maps of soil types, pH, seepage, vegetation maps and knowledge of the field situation (Fig. 3). The latter refers to field observations at a finer scale than could be inter-preted from maps.

Diversity

To test whether the macroinvertebrate diversity of water bodies in Korenburgerveen was higher than that of water bodies in other bog remnants, a comparison was made between water bodies within the same range in water chemistry. To this end, a principal component analysis (PCA) was applied to water chemistry data. All water bodies at Koren-burgerveen that were outside the water chemistry range of the water bodies in the other raised bog remnants were excluded from the comparison. This excluded all mesotrophic water bodies except for two very weakly buffered bodies, and all water bodies in the Salix-Betula forest except for one acid water body. All bog pools at Korenburgerveen were within the water chemistry range.

We calculated the α-diversity (average number of species: S_{mean}), β-diversity (Whittaker, 1960) and γ-diversity (using the method by Karakassis, 1995) for each of the seven bog remnants. The method proposed by Kay et al. (1999) was used to calculate the number of samples (N^*) needed before an additional sample added less than one species. Species accumulation curves provide the combined effect of average species number (α-diversity), species turnover (β-diversity) and the total number of species (γ-diversity) and visualise the biological diversity. We therefore calculated species accumu-lation curves using BioDiversity Professional Beta 1

Table 1. Differences in physical and chemical conditions between the different water types

Type	Subtype	Code	# Water bodies	pH	Alkalinity (meq l⁻¹)	o-PO₄³⁻ (µmol l⁻¹)	NO₃⁻ (µmol l⁻¹)	NH₄⁺ (µmol l⁻¹)	Size (m²)	Depth (cm)	Shading (%)	Temporary (0/1)
Bog pools	Large bog pools	B1	6	3.7±0.0	0.00±0.00	1.4±0.4	4.3±0.5	16.1±5.5	34±14	0.5±0.2	27±8	0.0±0.0
	Small bog pools	B2	6	3.8±0.1	0.00±0.00	1.0±0.2	4.8±0.5	40.9±12.4	16±8	0.5±0.1	37±8	0.2±0.2
	Small, shaded bog puddles	B3	6	3.8±0.1	0.00±0.00	1.6±0.4	12.3±5.3	44.7±11.7	8±4	0.5±0.2	66±16	0.2±0.2
Water bodies in wet forests	Water bodies in Salix-Betula forests	F1	4	5.0±0.3	0.28±0.14	3.3±1.3	3.1±0.3	28.8±8.2	18±5	0.3±0.0	62±19	0.6±0.2
	Water bodies in Salix-Alnus forests	F2	9	6.2±0.2	1.69±0.33	1.3±0.4	32.7±19.7	41.3±15.9	24±6	0.3±0.1	61±13	0.3±0.1
Mesotrophic waters	Shallow mesotrophic puddles	M1	4	5.4±0.3	0.26±0.06	1.0±0.4	4.0±0.1	11.4±2.1	52±33	0.4±0.1	39±11	0.3±0.1
	Mesotrophic pools	M2	5	5.7±0.2	0.36±0.14	0.5±0.2	4.6±0.7	9.7±2.0	409±211	1.1±0.2	13±5	0±0
	Strongly buffered mesotrophic pools	M3	5	6.5±0.2	1.06±0.18	1.3±0.5	2.1±0.3	8.0±1.0	108±42	0.7±0.1	39±14	0.2±0.1

Averages ±standard error are shown.
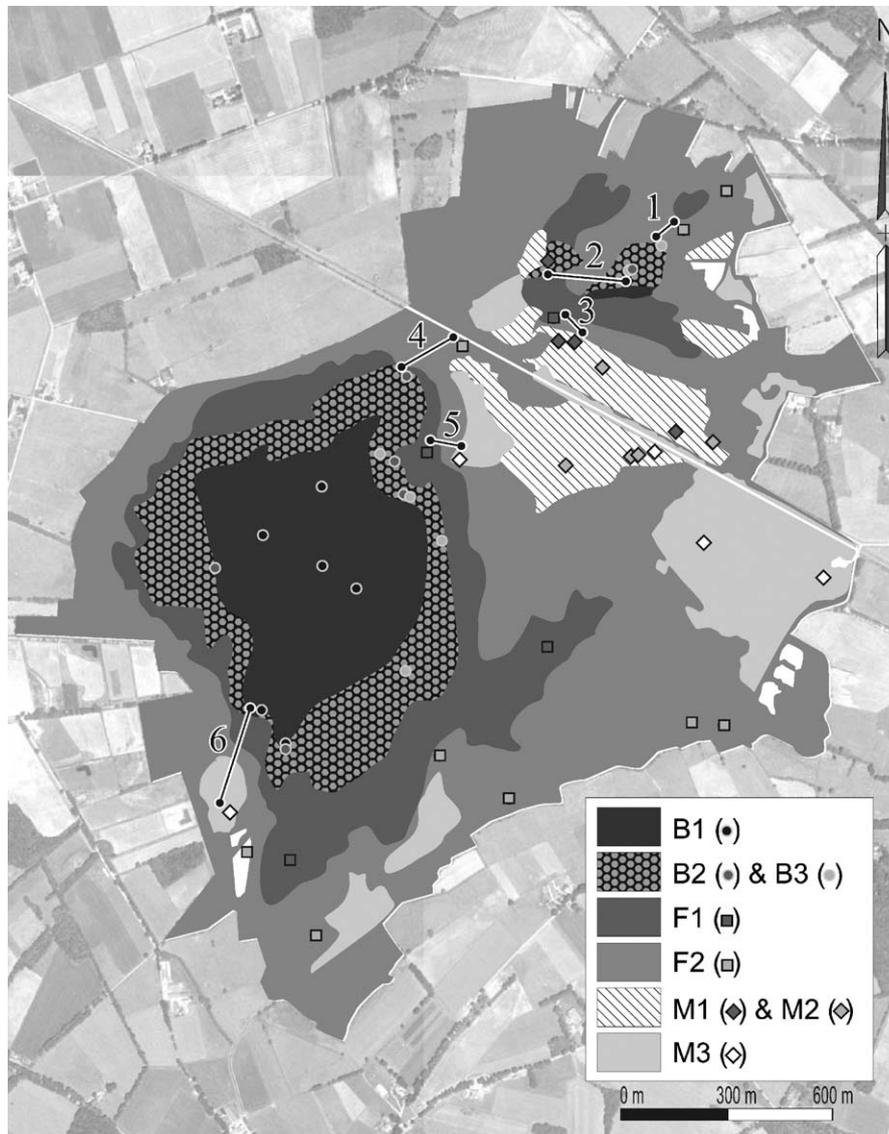
Figure 3. Sample locations and configuration of water types at Korenburgerveen. Connecting lines indicate pairs of adjacent sample points of different water types, which were compared in more detail (see Table 1 for a characterisation of the different water types).

(McAleece, 1997), based on averages of 500 random permutations of the sample sequence.

Spatial relations

To test whether adjacent water bodies were more similar in species composition than expected on the basis of differences in local environmental conditions, a measure of the dissimilarity in both environmental conditions and species composition was required. Dissimilarities in species composition between sites were calculated by performing a correspondence analysis (CA) on Preston transformed (Preston, 1962) macroinvertebrate abundance data. For each site, samples taken in spring

and autumn were pooled. Different life stages (larvae, nymphs and adults) of the same species were also pooled. To minimise the effects of differences arising from the sampling period, we entered whether or not a location was sampled in spring and in autumn as co-variables. Ordination scores on the first four axes (reflecting the most apparent differences in species composition) were used to calculate the dissimilarities, using the formula by Pythagoras (Eq. (1)). The eigenvalue was multiplied with the respective axis to correct for the differences in importance between axes.

Dissimilarities in environmental conditions between sites were calculated by grouping the local environmental factors into three groups: (i) water chemistry, (ii) vegetation (presence/absence of

plant species), and (iii) physical aspects (size, depth, etc.). For each group, a PCA was performed using all environmental variables within that group as input data. For each of these three groups, scores on the first two PCA axes (six PCA axes in total) were used to calculate the dissimilarities using the formula by Pythagoras (Eq. (1)). These six axes were considered to represent the major environmental gradients. To determine the relative importance of these six axes for macroinvertebrates, a CCA was run with Preston transformed macroinvertebrate abundances as species data and the six PCA axes as environmental data. Again, sampling periods were entered as co-variables. From this CCA, lamba1 scores were derived for each PCA axis which provide a measure for the amount of explanation the respective axis provided of the species variation. Therefore, lamba1 was used to weight the environment

areas, few intermediate pools (in terms of nutrient status and size, respectively) were sampled, resulting in a high N^* and a high β-diversity. The low α-diversity (S_{mean}) and low estimated γ-diversity (S_∞) at Tuspeel resulted in the second highest β-diversity. This indicates that, over a similar water chemistry range, species diversity is higher at Korenburgerveen at different scales (single water body, combinations of various water bodies and all water bodies within the water chemistry range).

Spatial relations at Korenburgerveen

The dissimilarity in environmental conditions and the dissimilarity in species composition were significantly correlated (Fig. 5; Pearson correlation: $r^2 = 0.36$, $p = 6.08 \times 10^{-5}$), demonstrating the importance of environmental conditions in structuring

$$D_{A-B} = \sqrt{(W1(O1_A - O1_B))^2 + (W2(O2_A - O2_B))^2 + \cdots + (Wi(Oi_A - Oi_B))^2}.$$

With D_{A-B} is the dissimilarity between samples A and B, Wi the (weighting factor; for macroinvertebrates, this is the Eigenvalue of ordination axis i; for environmental data, this is the Lambda1 score of ordination axis i), Oi_A the score of sample A on ordination axis i.

Centroids of all sites per water type were calculated by averaging the scores per ordination axis. The dissimilarity between pairs of adjacent sites was calculated. In addition, we calculated the dissimilarity between centroids of water types. All ordination analyses were performed using Canoco for Windows (Ter Braak & Smilauer, 1998).

Results

Differences in diversity between bog remnants

The Korenburgerveen bog remnant had the highest scores for all diversity indices we calculated (Fig. 4 and Table 2). N^* is a relative measure of the number of samples that are needed to get a complete species spectrum and was only slightly lower at Korenburgerveen than at Dwingelerveld and Bargerveen (Table 2). Relatively nutrient-rich and nutrient-poor water bodies were sampled at Dwingelerveld (although within the range of water quality considered) and relatively small and large water bodies were sampled at Bargerveen. In both

the macroinvertebrate assemblage. Adjacent pairs of sample locations from different water types (Fig. 3) were more similar in macroinvertebrate species composition to each other than the averages of the water types (centroids) to which they belonged (Table 3; $p = 0.046$; two-sided Wilcoxon signed rank test). This means that two water bodies had more species in common when they were adjacent.

This effect might have been caused by greater similarity in local environmental conditions between adjacent sites, but these proved not to be different from the centroids ($p = 0.600$; two-sided Wilcoxon signed rank test). When macroinvertebrate dissimilarities were divided by environmental dissimilarities (quotients) to compensate for environmental effects, adjacent sample pairs remained more similar in macroinvertebrate species composition to each other than the the centroids ($p = 0.046$; two-sided Wilcoxon signed rank test). This indicates that the greater overlap in species between adjacent water bodies cannot be explained by environmental conditions being more similar between these adjacent water bodies.

Discussion

Our comparison of macroinvertebrate diversity between bog pools in seven Dutch raised bog remnants shows that the Korenburgerveen remnant
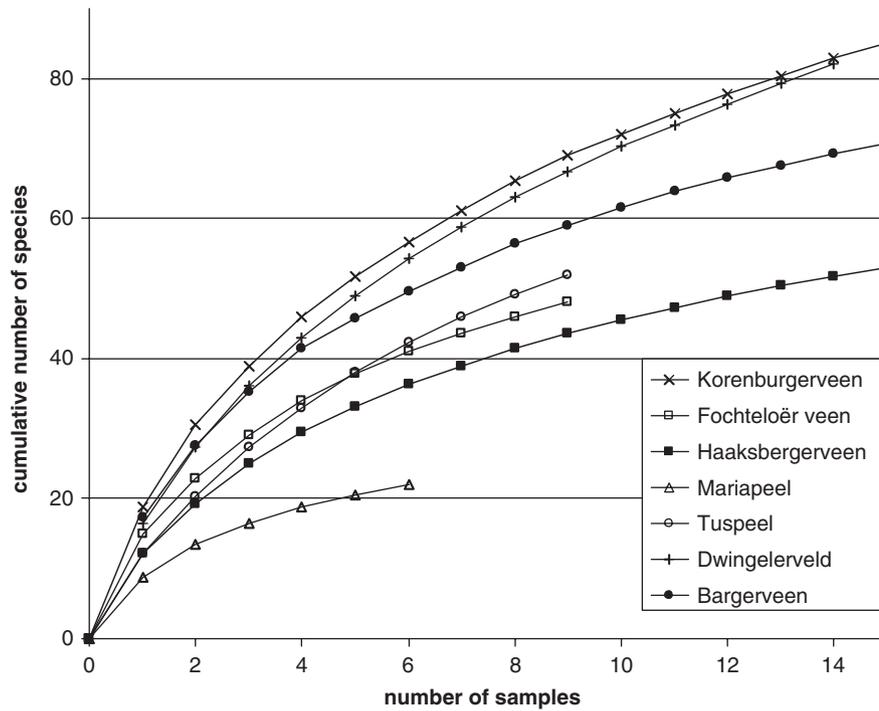
Figure 4. Species accumulation curves for each raised bog remnant. Curves are based on aquatic macroinvertebrates in bog pools only.

Table 2. Number of samples (N), average species number per sample (S_{mean}) and total species number (S_{total}) in the raised bog parts of the bog remnants sampled

	Measurements			Calculations		
	N	S_{mean}	S_{total}	S_∞	N^*	β
Korenburgerveen	40	18.9	115	114	13	5.04
Dwingelerveld	14	16.4	82	95	14	4.80
Bargerveen	20	17.3	78	80	15	3.64
Fochteloërveen	9	15.0	48	55	9	2.68
Haaksbergerveen	20	12.2	58	61	10	3.99
Mariapeel	6	8.7	22	25	6	1.89
Tuspeel	9	12.2	52	68	11	4.57

Calculations include the estimated number of species present (S_∞), the estimated number of samples (N^*) needed before an additional sample yields <1 extra species and the β-diversity.

had the highest scores on all diversity indices. Because the bog pools from all the raised bog remnants had the same range of water chemistry, the higher diversity at Korenburgerveen is most likely to have resulted from the interaction between the raised bog part and the surrounding ecosystems, which are more heterogeneous there. This means that bog pools situated in a heterogeneous landscape (as is the case at Korenburgerveen) have a higher diversity than bog pools located in more homogeneous landscapes.

The second question addressed in this paper concerned the importance of the distance between water bodies in determining species composition.

Our results show that adjacent water bodies were more similar in species composition than would be expected from the differences in local environmental conditions. These results are in line with the expectation that the exchange of individuals will be greater between adjacent water bodies. This means that the chance for a species to be present in a water body depends partly on the presence of nearby populations. Thus, it is not only local environmental conditions, but also the spatial configuration that plays an important role in determining the species composition. The importance of this factor probably increases with increasing heterogeneity.
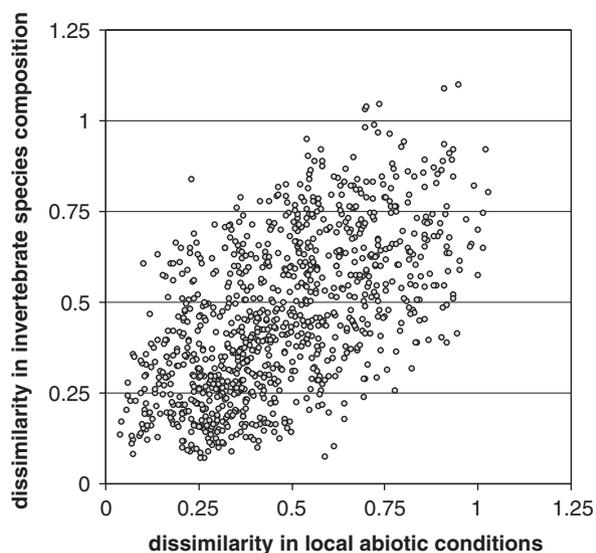
Figure 5. Pairwise comparisons showing the relation between dissimilarity in local environmental conditions and the dissimilarity in macroinvertebrate species composition. Plot is based on all water bodies sampled at the Korenburgerveen bog remnant.

One can argue that particular combinations of water type will be used by many species, whereas other combinations will be used by few species. As a result, differences in dissimilarity could depend largely on the combination of water types being compared. We compensated for this effect by comparing the dissimilarity between a combination of adjacent water bodies and the average dissimilarity for this combination of water types (centroids). Other sources of variation included: (i) spatial configuration, which was different for each water body, (ii) scale, as each species operates at its own scale level and (iii) the catch efficiency of the sampling method being less than the theoretical 100%. These sources of variation notwithstanding, a significantly higher similarity in species composition was found between adjacent water bodies, strengthening the validity of this finding.

What can we conclude about the effect of landscape heterogeneity on aquatic macroinvertebrate assemblages and macroinvertebrate diversity? It is already known that a landscape with more habitat types (higher habitat diversity) results in the presence of more species (e.g. Huston, 1979; Kerr, Southwood, & Cihlar, 2001), as each habitat type provides opportunities for additional species. However, this additive effect cannot explain why bog pools with the same water chemistry range harbour more species when they are situated in a heterogeneous landscape. Thus the species diversity in heterogeneous landscapes (i.e. those with a combination of different parts) is greater than the

Table 3. Degree of dissimilarity between pairs of adjacent sample locations (pairs are shown in Fig. 3) and degree of dissimilarity between centroids of the corresponding water types

Adjacent sample pairs				Water type centroids			
Combination no.	Dissimilarity invertebrate assemblage	Dissimilarity environmental conditions	Pair quotient	Water type combinations	Dissimilarity invertebrate assemblage	Dissimilarity environmental conditions	Water type quotient
1	0.40	0.46	0.87	B3–F2	0.64	0.61	1.05
2	0.15	0.31	0.47	M1–B3	0.45	0.41	1.10
3	0.28	0.28	0.99	M1–F1	0.26	0.27	0.96
4	0.41	0.74	0.55	F2–B2	0.67	0.62	1.08
5	0.18	0.32	0.56	M3–F1	0.34	0.38	0.90
6	0.44	0.79	0.56	B1–M3	0.53	0.75	0.70
Avg.	0.31	0.48	0.67		0.48	0.51	0.97

Both dissimilarity in environmental conditions and dissimilarity in macroinvertebrate species composition are shown.

total number of species that would be present if the individual parts were separated; i.e. the whole is more than the sum of its parts. This effect can arise when specific combinations of habitat types provide opportunities for new species.

An analysis of the spatial relations at Korenburgerveen supports the importance of combinations of habitats (habitat configuration). We propose three mechanisms that could explain this increase in biodiversity. First, greater heterogeneity results in the presence of more gradients (i.e. gradual transitions in habitat quality), thereby facilitating species with a narrow niche width, which depend on specific conditions that occur only in a gradient (mechanism 1). In effect, a new habitat type (the gradient itself) is present. Second, the presence of a range of adjacent habitat types can result in a mosaic of habitat types (habitat configuration) facilitating species that depend on combinations of two or more habitat types (e.g. during different life stages) (mechanism 2). This is an example of habitat complementation (Dunning, Danielson, & Pulliam, 1992). In a study of the butterfly *Maniola jurtina*, Ouin, Aviron, Dover, and Buirel (2004) demonstrated differential use of patches for different functions, such as feeding and resting. In our study, species with such a multi-habitat use would lower the dissimilarity in species composition between adjacent pools, as larval and adult life stages were pooled. For these species, the different water types have to be located at a traversable distance. Third, a heterogeneous landscape can harbour more species when heterogeneity decreases the extinction rate (mechanism 3). A lower extinction rate can result in an equilibrium state with a higher diversity (MacArthur, 1972). This may arise when: (i) a heterogeneous spatial arrangement of suitable habitat patches (habitat configuration) spreads extinction risks for species living in metapopulations (species go extinct only in one habitat patch, which can later be recolonised from other patches) or when (ii) the presence of different habitat types and gradients in a heterogeneous landscape prevents a disturbance from having the same effect on all types of habitat patches (habitat diversity). As a result, species occurring in different types of habitat patch can survive when only a subset of the patches becomes (temporarily) inhospitable. In a study of the grasshopper *Bryodema tuberculata*, Stelter, Reich, Grimm, and Wissel (1997) demonstrated that this species can persist in river floodplains by surviving catastrophic flood events in old gravel bars (suboptimal patches) and subsequently colonising newly created gravel bars (optimal patches) from these suboptimal patches.

An alternative explanation for the higher diversity at Korenburgerveen could be the mass effect (Shmida & Wilson, 1985), which states that a high local species richness can be the result of immigration from adjacent but dissimilar habitats. Species found in the oligotrophic bog pools at Korenburgerveen, but not in other remnants, may thus either be abundant in adjacent mesotrophic and eutrophic pools (mass effect) or may depend on the landscape heterogeneity (synergistic effect). It is difficult to distinguish between these effects. However, some species characteristic of raised bogs were found only at the oligotrophic pools at Korenburgerveen (e.g. *Lasiodiamesa gracilis* Kieffer, a rare chironomid; Verberk, Van Duinen, Moller Pillot, & Esselink, 2003), so their presence cannot be explained by the mass effect. Other species, for which bog pools are a suboptimal water type and for which the mass effect could be a valid explanation, may still depend on heterogeneity for population persistence, as they can locally survive in suboptimal habitats when the optimal habitat becomes temporarily unavailable (e.g. due to drought or the invasion of predators) (mechanism 3).

The importance of heterogeneity for population persistence was also suggested by Moller-Pillot (2003) in his study of the headwater catchment of the Roodloop stream, an unpredictable highly dynamic system. The level of specialisation of a species is usually defined in relation to the affinity with its environment, but some species may be mobility specialists. These species invest great resources in mobility, enabling them to use patches whose suitability is limited in space and time. These species may depend on landscape heterogeneity for population persistence. During the 10-year period of Moller-Pillot's study, a decline in many species was noted, including very common species such as *Dytiscus marginalis,* which was attributed to decreasing spatial variation.

What are the implications of our results for conservation and restoration? Heterogeneous landscapes represent biodiversity hotspots due to the additive effect, and they may also provide a safe haven for species that are not found in more homogeneous landscapes because they depend directly on heterogeneity (mechanisms 1 and 2). Conservation aims to protect biodiversity and restore natural processes (Bal et al., 2001). Due to their extreme environment, raised bog ecosystems are inhospitable to many species (Peus, 1923). The species present are highly specialised to cope with these conditions. It could therefore be argued that a strict focus on the restoration of the raised bog centre (the most extreme environment) is

justified, because this would result in high occurrences of rare and characteristic species, even though it creates a homogeneous landscape with low overall biodiversity values. However, this conclusion is incorrect, as more intact bog landscapes have a high landscape heterogeneity with transitional mire and lagg zones (Schouten, 2002; Wheeler & Proctor, 2000). 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). A study of aquatic macroinvertebrates in an Estonian bog 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 higher nutrient concentrations (Smits et al., 2002), while others selectively reproduced in temporary pools (Van Duinen, Dees, & Esselink, 2004). Even though the average number of species per water body was lower in Estonia than in the Dutch bog remnants, the species accumulation curve was steep, indicating a high β-diversity in intact raised bog systems (Van Duinen et al., 2002).

Conservation and restoration strategies should, therefore, not focus on increasing the size of only a single habitat type, but on conserving and strengthening landscape heterogeneity. This can be achieved by strengthening the processes that underlie this heterogeneity (e.g. variation in hydrological conditions arising from differences in seepage, infiltration and water flow). Restoration measures may result in a decline of landscape heterogeneity when large parts of an area are influenced (e.g. by large-scale rewetting measures) or when the measures cause major changes, which act as a disturbance. In nature reserves of high ecological value, these detrimental effects should be avoided.

The conservation and restoration of aquatic macroinvertebrates requires that a temporary or permanent loss of water types or rapid shifts in the spatial configuration are avoided (as was also emphasised by Van Duinen et al., 2003). One option to try and achieve management goals is by taking measures outside the reserve, for example restoring the regional hydrology by reducing drainage (filling in ditches) and increasing infiltration (by logging trees). However, internal measures may still be necessary. In such cases, 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). Another option is a phased implementation of the measures, changing only small parts at a time. This may allow local populations to recover from disturbance or recolonise from adjacent unchanged locations.

Monitoring the reaction of the species to restoration measures is a necessary tool to determine how to proceed with such measures. Knowledge about the water types that harbour important breeding habitats and the water bodies that represent important stepping stones for species is essential in choosing the optimal restoration strategy. Based on monitoring results, measures can be adjusted or partially reversed to optimise the recovery process. This approach will conserve populations in the short-term and restore characteristic plant and animal species assemblages in the various parts of landscape in the long-term (Schouten, Schouwenaars, Esselink, Lamers, & Van der Molen, 1998).

Acknowledgements

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