Matching species to a changing landscape

-Aquatic macroinvertebrates in a heterogeneous landscape-

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To curious people

Contents

The ninespine stickleback (Pungitius pungitius) can avoid competition by tolerating harsh conditions. Photo: Wilco Verberk.

Chapter 1

Introduction

Verberk WCEP

Scope

Human activities profoundly influence our landscapes today. Changes in land use, acidification, desiccation and eutrophication have resulted in a biodiversity crisis (Kerr & Currie 1995; Heywood & Watson 1995; Dudgeon *et al.* 2006). Local extirpation of a species may result from each of these human activities directly, or may be brought about indirectly, for example by creating more favourable conditions for its competitors or predators. These different causes are not mutually exclusive, but may act in concert or even augment each other. For example, an increased local extinction risk due to the effects of decreased habitat suitability may be exacerbated if opportunities for recolonisation are reduced, for instance by habitat isolation.

To counter the negative effects of degradation and to restore the original biodiversity, it is vital to identify the causes underlying this loss of species. This issue was addressed in a case study on the aquatic macroinvertebrates in lentic freshwater habitats of the Korenburgerveen, a heterogeneous bog remnant located in the east of the Netherlands (Fig. 1). Desiccation is a major problem in this and other bog remnants and constrains the growth of *Sphagnum* moss, which is an ecosystem engineer (van Breemen 1995; Schouwenaars *et al.* 2002). To promote the growth of *Sphagnum* moss, restoration

Figure 1 Various situations in the Korenburgerveen, illustrating the variety in water types. Left: acidic bog pool, dominated by common cotton-grass (*Eriophorum angustifolium*) and peat moss (*Sphagnum* spp.). Upper right: mesotrophic water body with bulrush (*Typha latifolia*) and broad-leaved pondweed (*Potamogeton natans*). Lower right: Wet alder carr forests with black alder (*Alnus glutinosa*) and water violet (*Hottonia palustris*).

plans in bog remnants frequently involve the construction of dams. In this way compartments are created where rainwater is retained and water tables are raised over large areas. But one may ask if this restoration strategy also effectively restores the environmental conditions required by the original aquatic macroinvertebrate species.

Knowledge on the relationship -or '*match*'- between a species and its environment is needed to understand the impact of degradation and to derive sound possibilities for restoration (Southwood 1977; Fig. 2). This thesis describes the results of a quest for this knowledge.
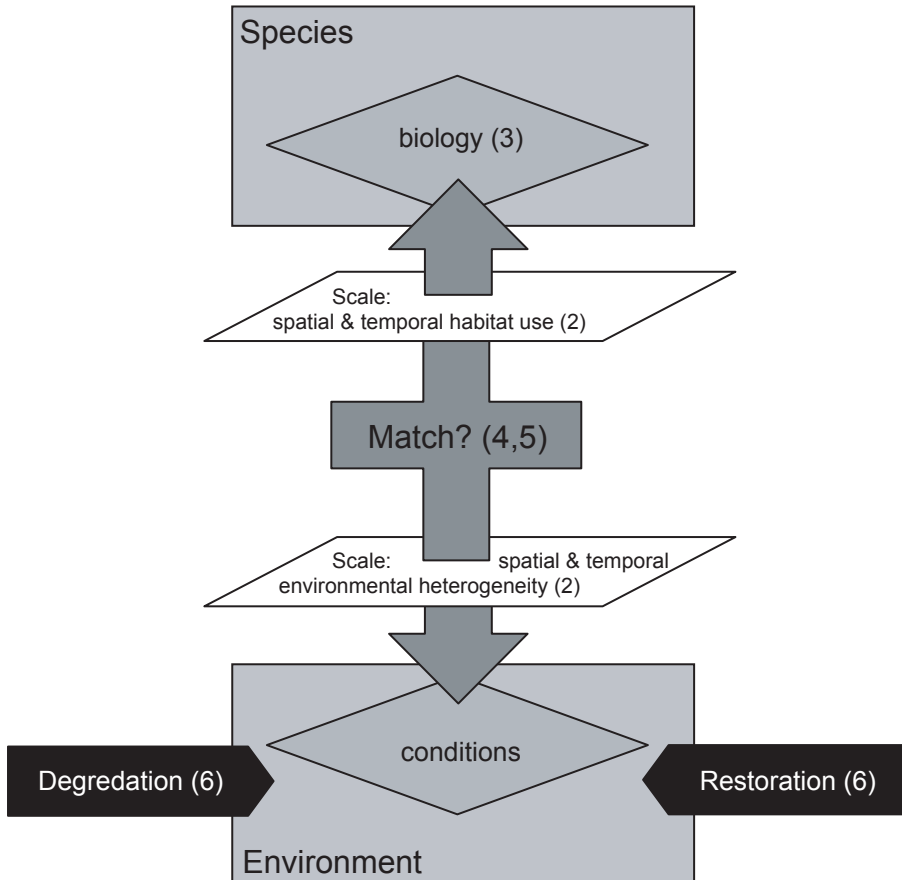
Figure 2 Schematic representation of the match between species and environment. Both species' requirements and environments' resources are scale dependent. Effects of degradation and restoration may influence this match by changing the environment. Aspects dealt with in the following chapters are indicated with numbers.

Matching species to changing landscapes

The match between a species and its environment is complex. What constitutes a favourable environment differs between species, depending on their requirements. In addition, species may use their environment on different spatial scales. Such differences

can also exist between different life stages of the same species. Likewise, environmental heterogeneity is a key element of a landscape and may occur at any spatial scale. Additionally, environmental conditions vary in time. Thus, both the requirements of a species and the environmental conditions often vary in time and space (*e.g.* during a species' life cycle), making the match between the two highly dependent on scale (*e.g.* Wiens 1989; Levin 1992; Fig. 2).

When trying to explain differences in species assemblages between locations or periods, the large variety in species-environment relationships presents a problem. Which environmental conditions are relevant for which species and at what scale level? Individuals of a species need to obtain resources to survive until they have successfully reproduced. In the course of evolution, species have developed physiological, morphological and behavioural traits to deal with environmental conditions. Environmental conditions include both abiotic conditions (*e.g.* high acidity, hypoxia) and other species (*e.g.* competitors, predators). A species trait is here defined as any morphological, physiological or phenological feature measurable at the individual level, from cell to the level of the whole organism, without reference to the environment or any other level of organisation (Violle *et al.* 2007). Examples include a chitinous exoskeleton, diapausing eggs, parental care, a large body size and a short development time.

Because species traits determine a species' ability to deal with environmental conditions and changes therein, species traits can be seen as the causal mechanisms underlying species-environment relationships (*e.g.* Keddy 1992; McGill *et al.* 2006). Species traits are not independent, but may be interrelated through trade-offs, with investments in one trait leaving less resources available for investments in another trait. Alternatively, investments in one trait may reduce costs or increase benefits of investments in another trait. For example, the lamellae of larvae of damselflies are used for both respiration and locomotion. With these interrelations between species traits it may be possible to define 'sets of co-adapted species traits designed, by natural selection, to solve particular ecological problems', which are termed life-history tactics by Stearns (1976). In this way, species with similar mechanistic explanations may be grouped in life-history tactics, thereby reducing the variety in species-environment relationships to a manageable number of key relationships.

Goal

The goal of this thesis is: "*to develop, apply and evaluate a method based on species traits and their interrelations by which relationships between aquatic macroinvertebrate species and their environment can be explained and aggregated to a manageable number of key relationships*". This method provides insight in a species' ability or inability to cope with changes in environmental conditions, and can therefore be used in matching species to a changing landscape.

Outline and research questions

The central question of this thesis is: "How to make sense of the large variety in species-environment relationships?". This is a fundamental question in community ecology (Hutchinson 1959; Southwood 1977; Lawton 1994). For aquatic macroinvertebrates in a bog landscape, the answer to this question can be used in applied issues such as determining how degradation has had an impact on species assemblages and deriving possibilities for successful restoration. To answer the central question, an approach from

a species perspective and an environmental perspective was used. The structure of the thesis and the main research questions are shown in figure 3.

To relate species composition and species richness to environmental conditions, the species assemblages of various bog remnants were compared. The results of this field survey are described in Chapter 2. Special emphasis was placed on the relation between environmental heterogeneity and species diversity. This is relevant because bog remnants harbour many aquatic macroinvertebrate species, which may depend on the environmental heterogeneity (van Duinen *et al.* 2003). The degrading effects of acidification, desiccation and eutrophication have decreased environmental heterogeneity by causing persistent and similar changes over large areas. This results for example in a vegetation dominated by purple moor grass (*Molinia caerulea*) or soft rush (*Juncus effusus*). The decrease in environmental heterogeneity itself can affect animal species such as aquatic macroinvertebrates, which may depend on a combination of different places to complete their life cycle. For example, a number of species require different water bodies, or different parts of a water body for hibernating, foraging and reproduction (Verberk *et al.* 2005).

To understand how species are adapted to deal with the various problems and opportunities present in their environment an alternative approach is taken, focussing on species and their traits. Information on species traits of aquatic macroinvertebrates was compiled and synthesised (Chapter 3). I studied how life-history tactics can be defined based on interrelations between species traits and the function of trait combinations (*e.g.* reduced egg mortality, speed up development, spread risks). Such life-history tactics should represent a species' integrated response to functional constraints of the environment. This was tested in Chapter 4.

Next, life-history tactics were applied to a fundamental and an applied problem in ecology. The general observation that locally abundant species are also widely distributed is studied from a life-history tactic perspective (Chapter 5). Explanations for this positive interspecific abundance-occupancy relationship focus on the role of (meta)population dynamics and a species' niche. Both these and other explanations can be related to differences in species traits, which determine a species' ability to deal with environmental conditions on a local and regional scale. Therefore, life-history tactics were used to generate and test predictions with respect to a species' abundance and occupancy. I return to bog remnants and the effects of restoration measures on aquatic macroinvertebrates in Chapter 6. Life-history tactics were used to relate changes in species assemblages of aquatic macroinvertebrate to changes in environmental conditions. Similar to degradation, large scale rewetting may result in a homogenisation by bringing about similar changes over large areas. This hypothesis was tested by studying changes in species richness and tactic composition following rewetting measures.

Finally, a synthesis of the preceding chapters is given in Chapter 7. It describes how life-history tactics may stimulate progress in the field of community ecology and how information on a species' life-history may guide efforts to restore the heterogeneity and biodiversity of a landscape.
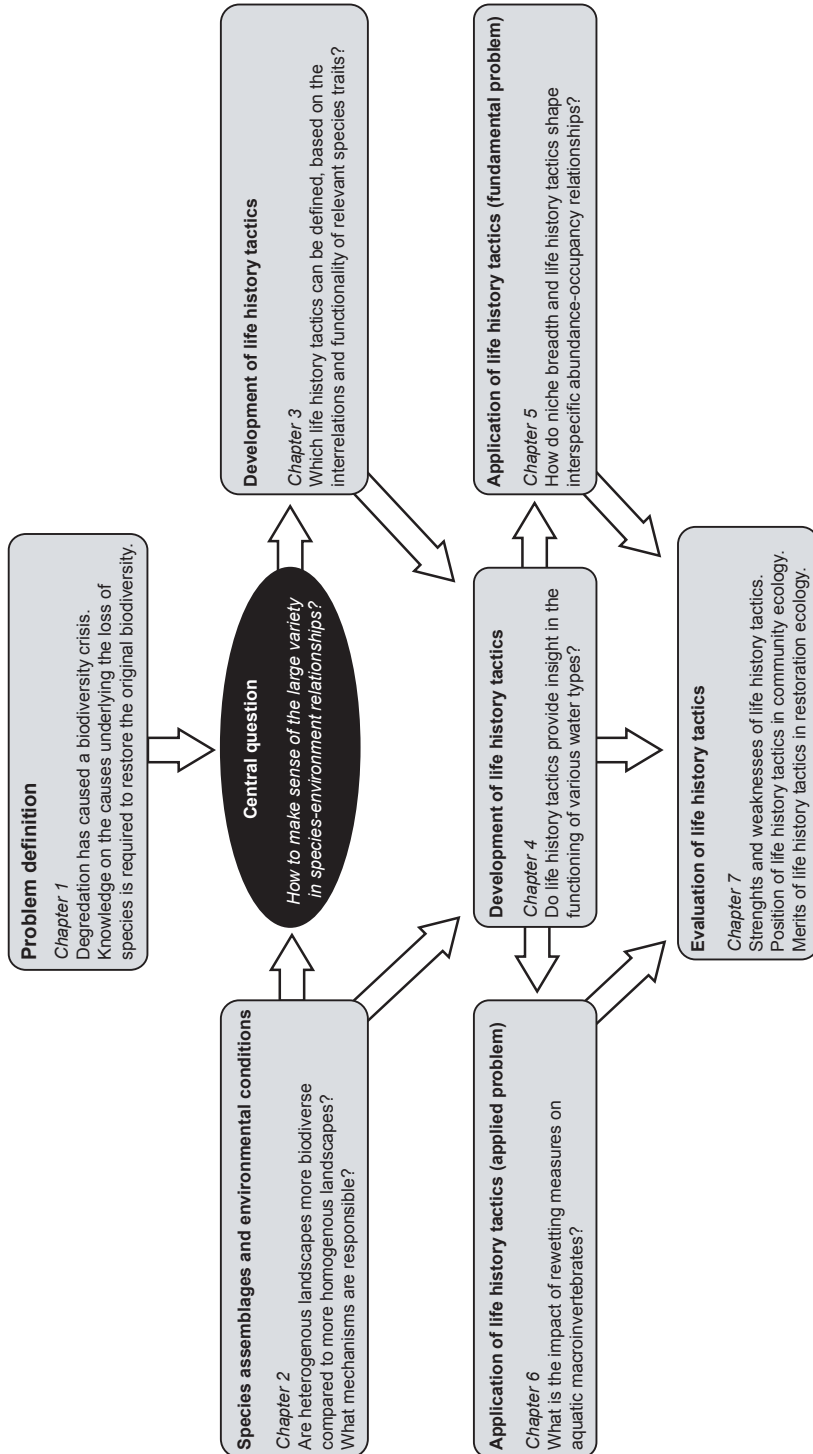
Figure 3 The structure of the thesis and the main research questions dealt with in each chapter.

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The Korenburgerveen reserve, showing a combination of an aerial photograph and a vegetation map.

Chapter 2

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

Verberk WCEP, GA van Duinen, AMT Brock, RSEW Leuven, H Siepel, PFM Verdonschot, G van der Velde & H Esselink

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 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 *et al.* 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 (*e.g.* reproduction, hibernation and foraging). 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
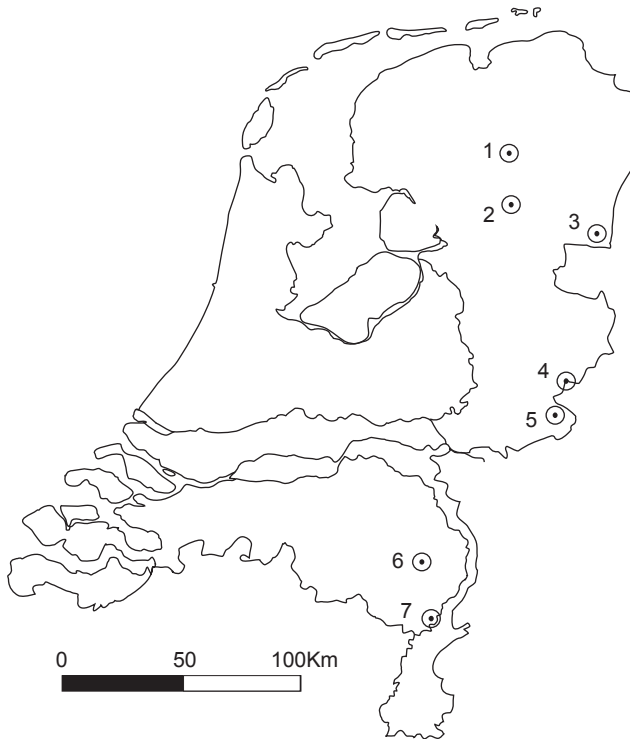
Figure 1 Locations of sampled raised bog areas in the Netherlands. 1. Fochteloërveen, 2. Dwingelerveld, 3. Bargerveen, 4. Haaksbergerveen, 5. Korenburgerveen, 6. Mariapeel, 7. Tuspeel.

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. 2). Earlier studies have shown that Korenburgerveen offers a large variety of water types and a high diversity of water beetles (Verberk *et al.* 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 & Proctor (2000), and were enriched by atmospheric nitrogen deposition and peat mineralisation, 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. 3). The first dataset comprised samples taken from seven bog 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.
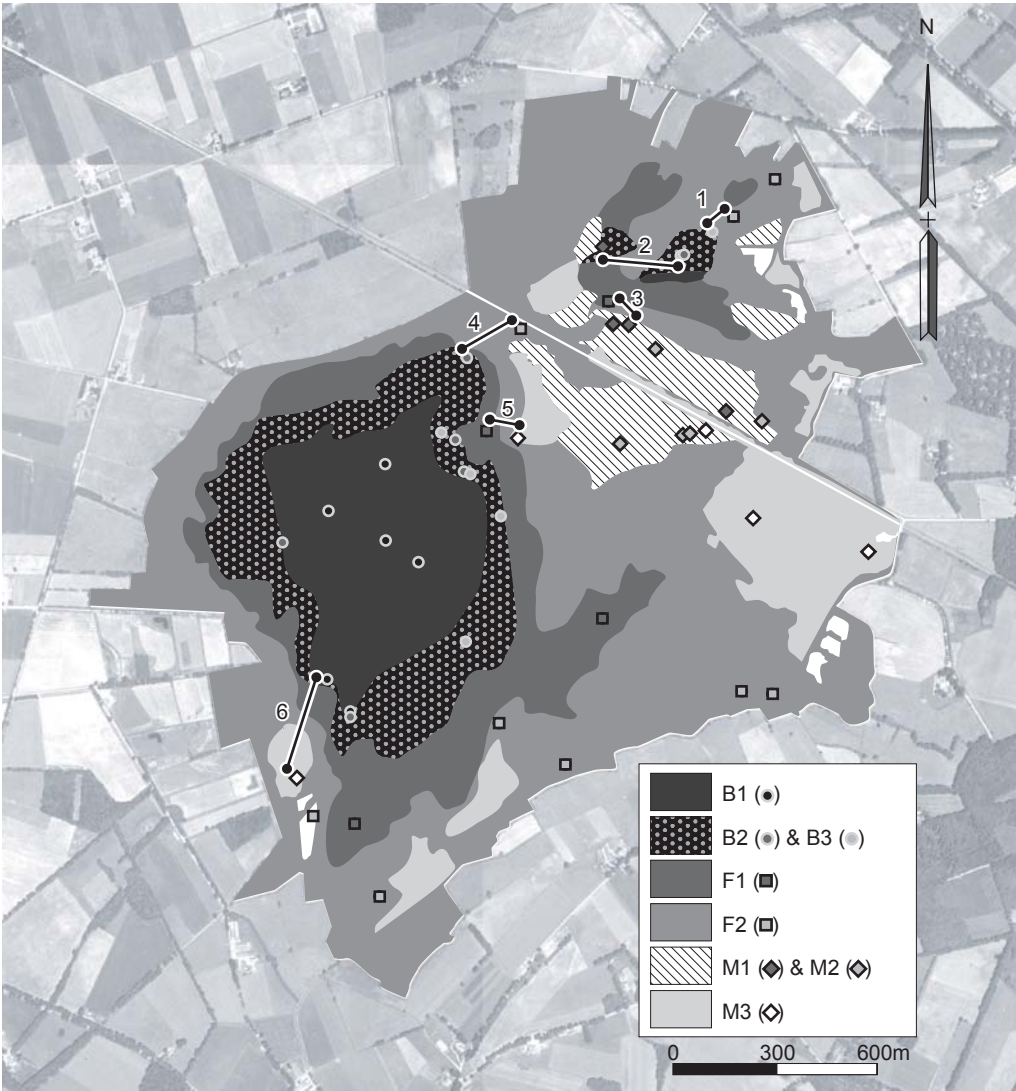

Figure 2 Sampling locations and configuration of water types at Korenburgerveen. Connecting lines indicate pairs of adjacent sample points of different water types, which were compared in more detail (see Table 1 for a characterisation of the different water types).

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: $\dfrac{\text{Dissimilarity in invertebrate species composition}}{\text{Dissimilarity in environmental conditions}}$ 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 $\sqrt{(\Delta \text{ Axis } 1)^2 + ... + (\Delta \text{ Axis } 4)^2}$ (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 $\sqrt{(\Delta \text{ Axis } 1)^2 + ... + (\Delta \text{ Axis } 6)^2}$

Figure 3 Schematic overview of the data used and analyses performed for each research question. See text for more details.

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 x 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 susceptibility to drying out, as well as in nutrient concentrations ($o\text{-}PO_4^{3-}$, 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. 2). The latter refers to field observations at a finer scale than could be interpreted 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 Korenburgerveen 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 1 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 accumulation curves using BioDiversity Professional Beta 1 (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

Table 1 Differences in physical and chemical conditions between the different water types. Averages ± standard error are shown.

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[1] (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

[1]Indicating the proneness to dessication of a water body, ranging from 0 (permanent) to 1 (temporary)

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 (*e.g.* size and depth). For each group, a Principal Component Analysis (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.

$$D_{A\text{-}B} = \sqrt{(W1^*(O1_A\text{-}O1_B))^2+(W2^*(O2_A\text{-}O2_B))^2+...+(Wi^*(Oi_A\text{-}Oi_B))^2}$$ (eq. 1)

With:
$D_{A\text{-}B}$ = Dissimilarity between samples A and B
Wi = (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 = 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 cumulative number of species (Fig. 4) and scored highest on all diversity indices (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 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}) at Tuspeel resulted in the second highest β-diversity. These results indicate that, over a similar water chemistry range, species diversity is higher
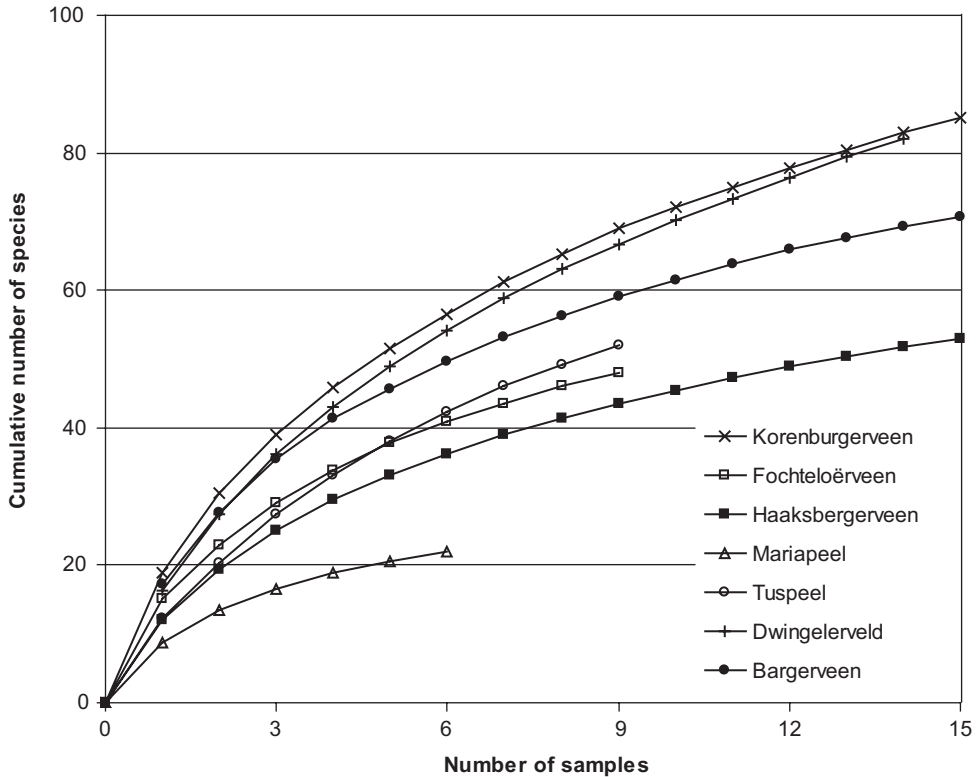
Figure 4 Species accumulation curves for each raised bog remnant. Curves are based on aquatic macroinvertebrates in bog pools only.

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 the macroinvertebrate assemblage. Adjacent pairs of sample locations from different water types (Fig. 2) 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

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

	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

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.
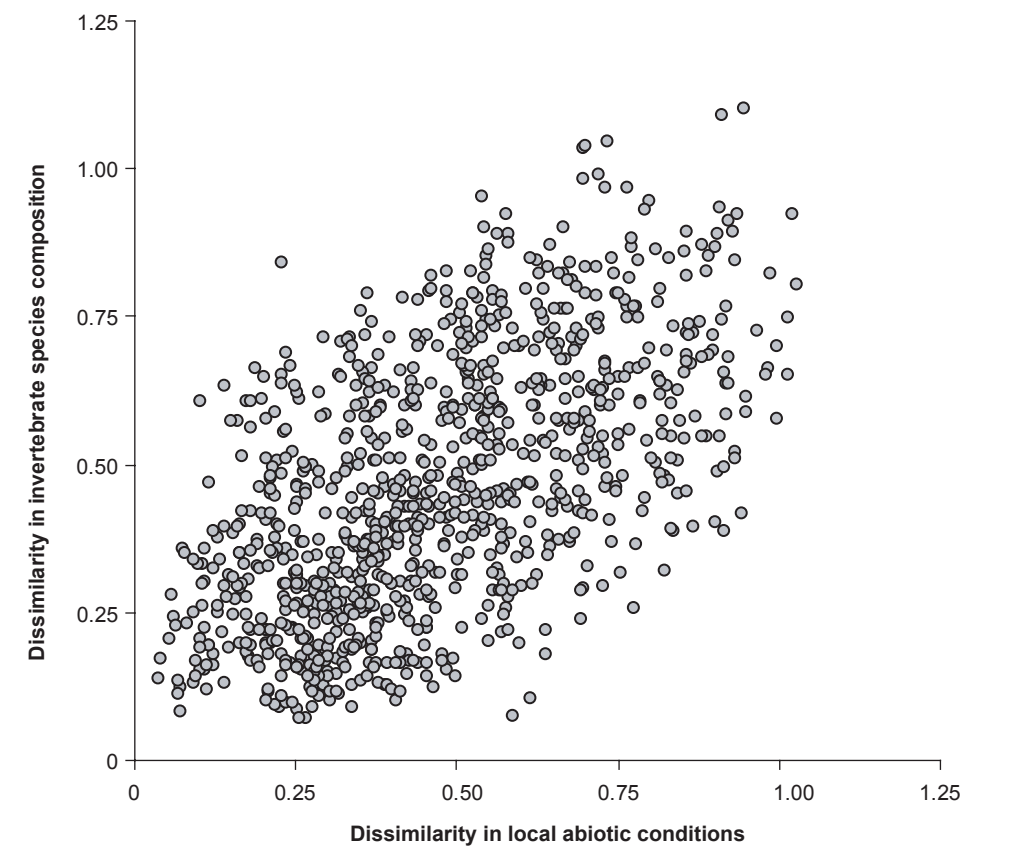

Figure 5 Pairwise comparisons showing the relation between dissimilarity in local environmental conditions and the dissimilarity in macroinvertebrate species composition. Plot is based on all water bodies sampled at the Korenburgerveen bog remnant.

Table 3 Degree of dissimilarity between pairs of adjacent sample locations (pairs are shown in Fig. 2) and degree of dissimilarity between centroids of the corresponding water types. Both dissimilarity in environmental conditions and dissimilarity in macroinvertebrate species composition are shown.

	Adjacent sample pairs				Water type centroids		
Combination nr	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
Average	0.31	0.48	0.67		0.48	0.51	0.97

Discussion

Our comparison of macroinvertebrate diversity between bog pools in seven Dutch raised bog remnants shows that the Korenburgerveen remnant 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.

One can argue that particular combinations of water types 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 *et al.* 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 total number of species that would be present if the individual parts were separated. In other words, 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 *et al.* 1992). In a study of the butterfly *Maniola jurtina*, Ouin *et al.* (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 *et al.* (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*, a rare chironomid;

Verberk *et al.* 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-Pilot'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 (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). 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 *et al.* 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 *et al.* 1998).

Acknowledgements

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European stag beetles (Lucanus cervus) combine a long larval development period (up to 8 years) with a short period during which adults are active (a few weeks). Photo: Wilco Verberk.

Chapter 3

Life-history tactics in freshwater macroinverte-brates

Verberk WCEP, H Siepel & H Esselink

Summary

Explaining spatial and temporal differences in species assemblages is the central aim of ecology. It requires a sound understanding of the causal mechanisms underlying the relationship of species with their environment. A species trait is widely acknowledged to be the key that links pattern and process, although the enormous variety of traits hampers generalisation about which combination of traits are adaptive in a particular environment.

In three steps, we use species traits to match species and environment, and chose lentic freshwater ecosystems to illustrate our approach. We first identify key environmental factors and select the species traits that enable the organism to deal with them. Secondly, we investigate how investments in these traits are interrelated through functional combinations and trade-offs. Thirdly, we outline thirteen life-history tactics, based on interrelations between species traits.

Species traits and environmental conditions are connected in life-history tactics, which represent different solutions to particular ecological problems. The numerical abundance of species aggregated to life-history tactics in a location gives direct information about how a particular environment is experienced by the species present. Life-history tactics can be used for (i) explaining differences in species assemblages either between locations or in different periods, (ii) reducing often very complex, biodiverse assemblages into a few meaningful, easily interpretable relationships and (iii) comparing water bodies found at a large geographical distance, which may comprise different regional species pools or span species distribution areas.

Life-history tactics are a potentially promising tool in environmental quality assessment programs and may guide future research by helping identify gaps in knowledge of a species' biology.

Introduction

Field observations on differences in species occurrence in space or time are at the heart of ecological research. However, the purpose of ecology goes beyond species identification and the documentation of differences and similarities in their occurrence. A problem of so-called taxon-based analyses, where differences and similarities in species occurrence are analyzed, is that they lack explanatory and predictive power (Lawton, 1999). Explaining the many patterns observed in nature is a central aim in ecology and requires an understanding of the causal mechanisms. These mechanisms provide a theoretical framework which explains how abiotic and biotic factors set limits to species occurrences, ultimately shaping ecosystems (Townsend & Hildrew 1994; Weiner 1995). Or as stated by Watt (1971): 'if we do not develop a strong theoretical core that will bring all parts of ecology back together, we shall all be washed out to sea in an immense tide of unrelated information'.

There is broad consensus that the way forward is to link pattern and process through species traits, in so-called taxon-free analyses (*e.g.* Keddy 1992; Doledec & Statzner 1994; McGill *et al.* 2006). A species trait is here defined as any morphological, physiological or phenological feature measurable at the individual level, from cell to the level of the whole organism, without reference to the environment or any other level of organisation (Violle *et al.* 2007). Previous studies either analysed traits separately (*e.g.* van Kleef *et al.* 2006; Statzner *et al.* 1994; Richards *et al.* 1997), or grouped species with similar suites of traits (*e.g.* Usseglio-Polatera *et al.* 2000; Ilg & Castella 2006).

This paper presents a fresh approach with the aim of defining groups of species with similar causal mechanisms underlying the species-environment relationships. Based on known relationships among species traits from life-history theory, species traits are combined to complex adaptations, termed life-history tactics. To emphasize the functional interlinkage, the term 'life-history tactic' is used, rather than 'suite of traits'. Stearns (1976) defines a life-history tactic as 'a set of co-adapted traits designed, by natural selection, to solve particular ecological problems'. With a functional approach, not every combination of traits has the same weight; evolution has selected for *adaptive* trait combinations. Species belonging to various systematic groups may solve the same ecological problem by different adaptations as set by the constraints of their basic morphology (Gould & Lewontin 1979; Felsenstein 1985). For example, when dispersal is necessary for a species' survival, it may solve that by active flight, or passive transport, such as phoresy or anemochory. The adaptive value of trait combinations is therefore context-dependent, related to both the environmental conditions and a species' basic morphology.

We illustrate our approach with lentic freshwater ecosystems. In temperate regions, the macro-invertebrate assemblages in lentic freshwater habitats are structured mainly by the transition from temporary to permanent water bodies, and from predation by invertebrates to that by fish (Collinson *et al.* 1995; Wellborn *et al.* 1996; Tonn *et al.* 2004). We focus here on fish-free, lentic freshwater bodies as they are rich in macroinvertebrates (Scheffer *et al.* 2006). Our example covers the following systematic groups: Tricladida, Hirudinea, Oligochaeta, Crustacea, Odonata, Hemiptera, Coleoptera, Diptera (Chironomidae, Dixidae, and Culicidae) and Trichoptera.

Here we ask which species traits are relevant in dealing with the key factors that determine the suitability of the environment for aquatic macroinvertebrates? Furthermore, how are these traits interrelated through functional combinations and trade-offs? And lastly, which life-history tactics can be defined, based on the interrelations among and the functionality of these relevant traits?

Key factors of environmental suitability and related species traits

A basic property of a habitat is that its suitability is subject to spatial and temporal variation. In his habitat templet, Southwood (1977) distinguished between habitat being favourable in time, now or later, and in space, here or elsewhere, giving rise to four quadrants. By doing so, he explicitly provided room for spatial differences in habitat favourability. Each quadrant has a different optimal response (Table 1): The optimal response in the here-now quadrant is resource dominance (breed now). When the habitat is favourable elsewhere, later or both elsewhere and later, the optimal response is dispersal (migration in space, breed elsewhere), persistence (migration in time, breed later) or a combination of both, respectively.

Table 1 Optimal responses in various environments with habitat suitability differing in space and time (after Southwood 1977).

		Space	
		Here	Elsewhere
Time	Now	Resource dominance	Dispersal
	Later	Persistence (diapause)	Dispersal & persistence

Examining temporal variation more closely shows that the duration of favourable periods, as well as the time interval between them, are important in shaping the optimal response (Townsend & Hildrew 1994). In addition, predictability is an important aspect of temporal variation (Stearns 1976). Persisting and breeding later, for example, is a far more optimal response when it is predictable that favourable periods are of sufficient duration (*i.e.* equal to or exceeding the generation time). Stearns distinguished between several additional responses being adaptive in environments where temporal variation in habitat suitability was either predictable (*e.g.* synchronised juvenile development) or unpredictable (*e.g.* long-lived adults capable of resorbing reproductive tissue). He found that when favourable conditions are unpredictable, many responses are non-fixed, characterised by a variance in oviposition and hatching. For instance in unpredictable environments, more small clutches or eggs are favoured over a few large clutches and long adult life time with delayed reproduction is favoured over short adult life time with early maturity (Stearns 1976). In effect, reproduction attempts are spread over a longer time period or more locations, thereby reducing the effects of stochasticity. Responding in such a way enables a species to spread the mortality risks and is termed risk spreading. The term bet-hedging is used in the case of a species hedging its bet by exhibiting contrasting responses (*e.g.* eggs with and without diapause), on which selection can act. This usually lowers average reproduction success, but minimises the chance of total reproductive failure.

Regarding space, the here-elsewhere demarcation of Southwood can also be further refined to better reflect the spatial variation in favourable habitat. The predictability of spatial variation, namely how probable is it that favourable habitat will be found elsewhere, depends on the distance between favourable locations and whether they are clumped together or widely distributed. If dispersal is needed, these aspects of spatial variation determine whether it is best to disperse over a short or a long distance, and whether new favourable locations are best reached through active or passive dispersal. Analogous to temporal variation, flight polymorphism can be recognised as a form of spatial bet-hedging.

A species' absence from a habitat may indicate that the habitat is unfavourable, but may also result from isolation, competition, predation or a combination thereof. Taking temporal variation into account, unfavourable periods may occur more frequently than the chance of recolonisation (Siepel 1996). Likewise, a species presence may indicate that a habitat is favourable, but may also result from source-sink dynamics (Pulliam 1988). In lentic freshwater bodies, factors such as drought, acidity, salinity or food quality determine a habitat's suitability for aquatic invertebrates. These factors may constrain habitat suitability continuously or they may fluctuate, either in a seasonal, predictable way or stochastically.

As there is temporal and spatial variation in a habitat, key factors shaping species' responses are the duration, degree and predictability of suitability of the habitat. In this framework, harshness of the environment is the inverse of its suitability, and intense competition is considered to occur most under benign, predictable and stable conditions. Rather than combining the various states of these key factors into a limited set of environmental situations and deriving the associated optimal response, we here use these environmental key factors to select those traits that enable an organism to deal with them and thus are relevant to base life-history tactics on. Scale and spatial heterogeneity are additional attributes of the environment, as scaling effects are universal in ecology (Wiens

1989) and inextricably linked to the spatial heterogeneity of the environment. Different species and even different life stages of the same species use their environment on a range of scales and their adaptations have a scale-dependent functionality (Verberk *et al.* 2005). For example, Statzner *et al.* (1997) report that many aquatic insects in temporary waters deposit their eggs within plants. Thus depending on the spatial scale, their environment is characterised by a low temporal variation (within plants) or a high temporal variation (temporary waters). This makes it difficult to link species and scale directly. However, there is an indirect link, as the predictability of variation in space and time depends on how it is perceived by an organism, which in turn is linked to species traits such as its mobility and development time. The scaling is thus integrated in the total life-history of a species. Therefore, scale and spatial heterogeneity are not directly included here to select traits on which to base life-history tactics, but must rather be seen as emergent attributes, which are included indirectly.

From relevant traits to tactics

Traits that are relevant in overcoming the main environmental constraints can be derived from the ideas of both Southwood (1977) and Stearns (1976). When a location is favourable for the duration of a single generation, each generation must either disperse to other locations or bridge the time period till the next favourable period by quiescence or diapause. When it is not likely that other favourable locations are close by, spreading of risk, *i.e.* increasing the number of offspring instead of a high *per capita* investment will be favourable. Alternatively, traits such as large eggs, brood care and long adult life span will be favoured on a highly favourable and predictable location, increasing a species'
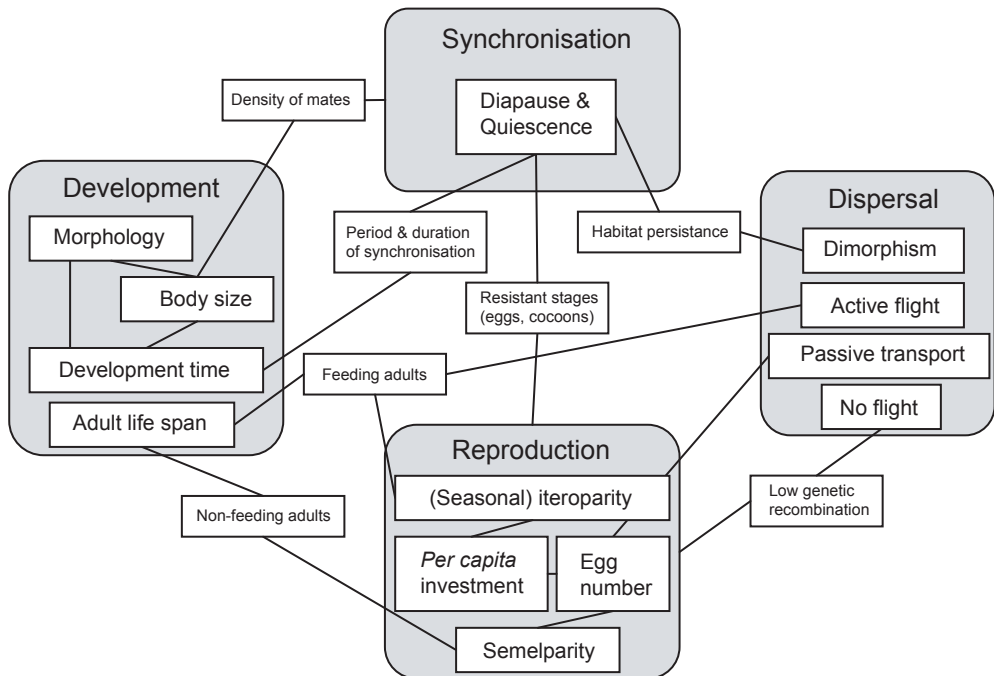

Figure 1 Overview of interrelationships between traits belonging to the four trait domains (shown in grey). Relationships are explained in the text.

persistence. On predictable harsh locations, a high persistence will be combined with a long juvenile development. Figure 1 presents the relevant traits in four main domains of traits (Siepel 1994): (i) reproduction, (ii) development, (iii) dispersal and (iv) synchronisation. These species traits are interrelated, both within and between domains. For each domain we discuss these intra- and interrelations, using species examples.

Reproduction
The large variation in aquatic macroinvertebrate reproduction is expressed in species traits such as egg size, egg number, brood care and how reproductive investment is distributed over clutches. These traits can be positioned on two different axes (Fig. 2). The first axis pertains to *per capita* investment. There is a well-known trade-off between egg size and egg number, with animals laying either many small eggs or a few large eggs (*e.g.* Berrigan 1991). A larger egg size effectively increases the *per capita* investment and is usually

Per capita investment in offspring

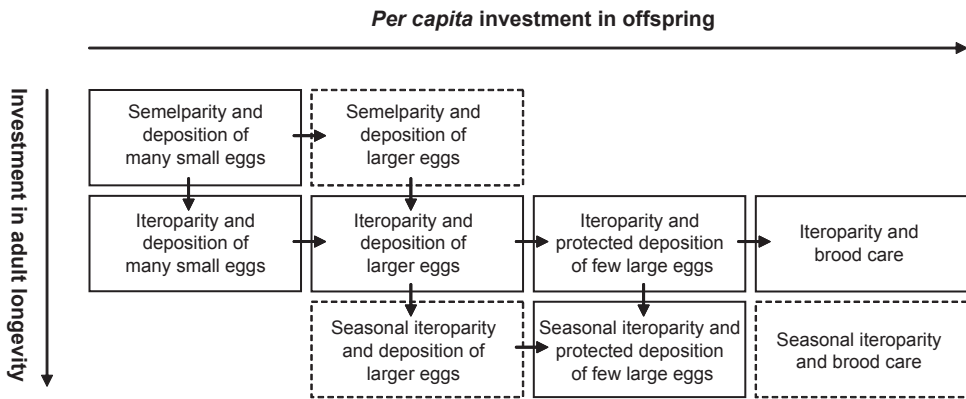| Semelparity and deposition of many small eggs	Semelparity and deposition of larger eggs		
Iteroparity and deposition of many small eggs	Iteroparity and deposition of larger eggs	Iteroparity and protected deposition of few large eggs	Iteroparity and brood care
	Seasonal iteroparity and deposition of larger eggs	Seasonal iteroparity and protected deposition of few large eggs	Seasonal iteroparity and brood care

Investment in adult longevity

Figure 2 Important traits for reproduction positioned along an axis of *per capita* investment and an axis of investment in adult longevity. Dotted squares represent rare combinations.

accompanied by increased protection of eggs (*e.g.* endophytical oviposition, which is an extra time investment) and brood care.

The second axis pertains to the investment in adult longevity and is related to the spatial and temporal spread of reproductive effort. At one end of the spectrum are the semelparous species, which oviposit once at a single location at a single time. These species usually have short-lived adults and a high reproductive investment (Stearns 1976). Reproductive investment decreases from semelparous species to iteroparous species, which have several oviposition events confined to one season, and further decreases in seasonally iteroparous species, which spread oviposition over several seasons (*e.g.* Braby & Jones 1995). A decreased reproductive investment is matched by an increased investment in adult longevity and also an increased investment in dispersal when oviposition is spread over different locations (*e.g.* Johnson 1969).

The disadvantage of fewer offspring, associated with a higher *per capita* investment, is offset by enhanced juvenile survival rates, resulting from egg protection and brood care (*e.g.* Thiel 1998). For example, dragonfly species such as *Brachytron pratense*, that oviposit within plants (endophytically) have fewer but larger eggs than species such as *Libellula depressa* that oviposit exophytically (Sternberg & Buchwald 1999). A high *per capita* investment is usually combined with iteroparity and seasonal iteroparity. For example, the

alder fly *Sialis lutaria*, oviposits in large batches (up to 2000) with no apparent protection or spread of reproductive effort (Grabow 2000), while *Helobdella stagnalis* has extensive brood care with protection and feeding of young and spreads reproductive effort over several successive batches (~50 eggs in one season; Kutschera & Wirtz 2001). Iteroparous species spread oviposition spatially, temporally or both and may combine such oviposition with egg protection and brood care. Although seasonally iteroparous species usually show egg protection, extensive brood care generally does not occur (Fig. 2), possibly because both a high *per capita* investment and a high investment in adult longevity presents a double investment (*e.g.* Cole 1954; Braby & Jones 1995). Furthermore, when juvenile survival relative to adult survival increases, for instance as a result of brood care, seasonal iteroparity will not be favoured (Stearns 1976).

In addition to the above mentioned reproduction traits, species may have different types of reproduction ranging from sexual (biparental and hermaphroditic reproduction) to asexual (automictic and apomictic thelytoky) reproduction, with concomitantly decreasing genetic recombination. Many snails, leeches and worms have poor dispersal capacities. They are also hermaphrodites and some are capable of asexual reproduction, suggesting that low dispersal and low genetic recombination are connected. Genetic recombination can be lower in more constant environments (Siepel 1994) and hermaphrodites and asexuals have a higher intrinsic rate of increase. Therefore, an asexual or hermaphroditic reproduction allows a resource dominance response, which works best in the here-now quadrant. Here, a change of habit may diverge from the proven optimal response and a change of location may require new responses.

Development

Species traits related to development in aquatic macroinvertebrate species are development time, growth rate, body size and adaptive morphology and physiology. Examples of the latter include long pointed mandibles for piercing prey, storage organs, impermeability of the cuticle, level of haemoglobin or respiratory organs such as long filamental gills or siphons. These developmental traits are obviously interrelated. The trade-off between body size and development time is well known, with resources being allocated either to growth or development (Abrams *et al.* 1996). Given a constant resource supply, allocating resources to development shortens development time, while allocating resources to growth lengthens development time, thus giving rise to either small individuals with an early maturation, or large individuals with a late maturation. When development needs to be completed within a limited time period or on a finite food supply, individuals tend to stay small, giving priority to investment in development over growth (*e.g.* Rowe & Ludwig 1991; Abrams *et al.* 1996).

Investments in morphological and physiological adaptations take additional energy investments, prolonging development time or reducing body size. Such investments also include energy storage by so-called capital breeders, enabling a rapid reproduction in adults (Bonnet *et al.* 1998). In some circumstances, species depend on a high food quality to use habitats of limited duration. For example, *Aedes punctor* inhabits temporary water bodies, limiting the time available for larval development. Short development times are achieved by a small body size and by feeding a high quality food source (*e.g.* algae and bacterial film, Cranston *et al.* 1987), which is readily available in temporary water bodies and in sufficient amounts. Resources are used primarily for growth and development, leaving emerging adults with almost no fat reserves. Adults feed on a high quality food

source, such as blood, which extends their life span and is easily converted to eggs. As a result, several batches of eggs can be oviposited in a short time, enabling them to exploit the short periods during which suitable habitat is available.

Many aquatic macroinvertebrates feed only as larvae and have non-feeding adults. These adults have a short lifespan and usually reproduce semelparous (Bonnet *et al.* 1998). For example, adults of the caddisfly *Triaenodes bicolour* live 1-10 days and deposit eggs in a single batch of 200-300 eggs (Higler 2005). Feeding adults have a longer lifespan, which is accompanied by iteroparity and seasonal iteropary. For example, the leech *Glossiphonia complanata* is one of the few seasonal iteroparous leeches and has a large body with six pairs of crop caeca, in which food is stored, enabling them to survive periods with low food availability, for example during overwintering (Dresscher & Higler 1982).

Species able to tolerate adverse conditions have relatively long development times, small body sizes or both. Such hardships include low food supply, which requires a high assimilation efficiency, or high salinity or acidity, which requires a high energy expenditure to maintain homeostasis. For example, cladocerans with a high assimilation efficiency displayed slower growth and reproduction rates, reflecting a trade-off between efficiency and power (Tessier & Woodruff 2002). Adverse conditions during juvenile developments may also induce facultative dispersal capacities such as the development of flight muscles in species that usually do not disperse by flight (van Schaick Zillesen & Brunsting 1984).

Dispersal

Aquatic macroinvertebrates can reach new sites through active flight or passive transport, such as phoresy and anemochory. This is rooted in a species' basic morphology, with most insects being capable of flight and most other groups, such as leeches, flatworms, worms and crustaceans being incapable of flight. Water fowl mediated dispersal (zoochory) is an important factor in the dispersal of aquatic organisms (Figuerola & Green 2002). In addition, some non-insect species are adapted to passive transport. For instance, juveniles of the water spider *Argyroneta aquatica* are capable of anemochorous dispersal through ballooning. Alternatively, in aquatic insects, the capacity for flight has been reduced to varying degrees. Some species are capable of flight for a short time window only (*e.g.* just after emergence such as the beetle *Agabus affinis*; Jackson 1955), other species have flying and non-flying morphs (*e.g.* the semi-aquatic bug *Gerris gibbifer*), and some species have lost flight entirely (*e.g.* the apterous females of the caddisfly *Enoicyla pusilla*).

Many species with active flight capabilities may cover larger distances passively by anemochory. On short distances, an active steering can take place. Flight capability trades off with reproductive traits via allocation of internal nutrients (Zera & Denno 1997), and reproduction usually takes place after migration, which Johnson (1969) termed the oogenesis-flight syndrome. Both dispersing and diapausing individuals are relatively unresponsive to stimuli, suggesting a regulation by similar physiological mechanisms (Tauber & Tauber 1981). Due to the linkages between dispersal, synchronisation and reproduction, information on dispersal can be inferred when viewed in conjunction with reproductive and developmental traits: Passive dispersal is expected to be associated with large numbers of eggs, to mitigate the low chance of successfully reaching new favourable habitat. It is more common among species with non-feeding adults and a small body size. Iteroparous and seasonal iteroparous species have a longer adult life span investing more in adult body size and flight capability. Investments in flight may constrain reproductive investment, but active dispersal enables species to select most favourable sites for (protected) oviposition.

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Flight polymorphism, in which case flying and non-flying individuals occur within a population, is known from aquatic Coleoptera and Hemiptera. Because these groups have aquatic adults, reproduction can be achieved without flight. Under these conditions, flightlessness is not an evolutionary dead end, permitting the development of flight polymorphism (Harrison 1980). Apterous morphs of the semi-aquatic bug *Gerris lacustris* developed faster than macropterous morphs (Vepsäläinen 1978). In addition, apterous morphs of *Gerris buenoi* and *Gerris pingreensis* had shorter preoviposition periods, leading to greater egg production over the first 20 days of reproductive life (Spence 1989). Polymorphism thus reflects a developmental trade-off; instead of morphological investments in wings and wing muscles, a decrease of development time is favoured (see also the paragraph on development). This allows a higher voltinism and gives apterous morphs a competitive advantage over macropterous morphs. Dispersal has the advantage of reaching and colonising new sites, but the disadvantage of dislodging a population from a site (especially in mobile species of Gerromorpha, which hibernate on land), which may be favourable in subsequent seasons. Polymorphism at the population level would be a logical adaptation, with the advantages of flight declining with increasing isolation and the advantages of flightlessness declining with decreasing duration or persistence of the habitat (Vepsäläinen 1978).

Synchronisation
Synchronisation concerns the timing of reproduction, development or dispersal and is therefore intimately linked to a number of species traits in these domains, such as adult life span, voltinism and developmental time. Synchronisation can be achieved by either slowing down or speeding up development. A faster development is known in the dragonfly *Sympetrum danae* that can skip a larval stage, resulting in adults emerging sooner, albeit smaller (Sternberg & Buchwald 1999). Quiescence and diapause can slow down or halt development.

Quiescence is a flexible mechanism with animals displaying low activity in response to and for the duration of adverse local conditions, such as low temperatures or temporary food shortage. In contrast, diapause is more rigid with a physiological basis (Tauber & Tauber 1981) and serves to bypass long term predictable adversities (for example summer drought or winter frost). External cues such as photoperiod and temperature sum are important in inducing and breaking diapause dormancy. Species wide synchronisation can therefore be achieved with diapause. Obligatory diapause cannot be averted and therefore precludes multivoltine life cycles (*e.g.* Saulich & Musolin 1996). Facultative diapause can be averted under the right set of conditions. For example, hibernating diapause in the semi-aquatic bug *Gerris odontogaster* usually occurs after solstice, but not before (Vepsäläinen 1978). Diapause can potentially affect only part of the population, termed partial diapause, which is a form of (temporal) bet-hedging. For example, eggs laid during early summer by the dragonfly *Somatochlora arctica* can hatch either within 4 weeks or enter diapause and hatch after more than 20 weeks. The proportion of diapausing eggs may reach values up to 20% (Sternberg 1995), thus hedging its bet of eggs hatching during summer when conditions may be too dry and eggs hatching next spring, lagging behind in development.

Synchronisation can solve different problems. Synchronisation to bridge periods of extremely harsh conditions usually occurs in resistant stages, which are mostly immobile stages such as the egg or pupal stage (*e.g.* Sota & Mogi 1992). For example, endophytical

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eggs of the dragon fly *Aeshna cyanea* overwinter in a diapause, hatching early in the next spring (Sternberg & Buchwald 1999). In contrast, egg diapause in the dragon fly *Sympetrum striolatum* only serves to bypass the summer period as most eggs hatch before winter (Ottolenghi 1987). Iteroparous and seasonal iteroparous species may also bridge unfavourable periods as adults (*e.g.* terrestrial hibernation or aestivation).

Synchronisation to match activity to coincide with favourable periods usually pertain to food availability and therefore concerns the larval stages. Unfavourable periods may occur predictably, such as winter harshness and summer drought, in which case synchronisation is best achieved endogenous. To bridge these periods egg diapause may be used. Synchronisation may also be related to non-environmental conditions such as mating with conspecifics, competitive advantages or predator satiation. Especially for species with short adult life span, synchronisation of emergence is important to increase chances of finding mates and satiation of predators.

With respect to finding mates, synchronisation becomes more stringent for species with low population densities. Allometric relationships are found for density, with larger species occurring -on average- in lower densities (Schmid *et al.* 2000). Keeping adult longevity constant, larger species are therefore expected to have a higher need to synchronise compared to smaller species. Chironomidae species have a short adult life span (<2 weeks), but show marked interspecific differences with respect to the period and duration in which adults are active. The majority of the species is multivoltine and the emergence of the first generation in spring proceeds more synchronised. Spring synchronisation is indeed more pronounced in larger species compared to smaller species (Fig. 3), assuming species achieve a better synchronisation when they overwinter in the final or near final stage. Also in the meniscus midges *Dixella* spp, the larger species, *Dixella aestivalis* and *Dixella autumnalis* show a higher degree of synchronisation with larvae occurring mostly in autumn and spring respectively (Disney 1999).

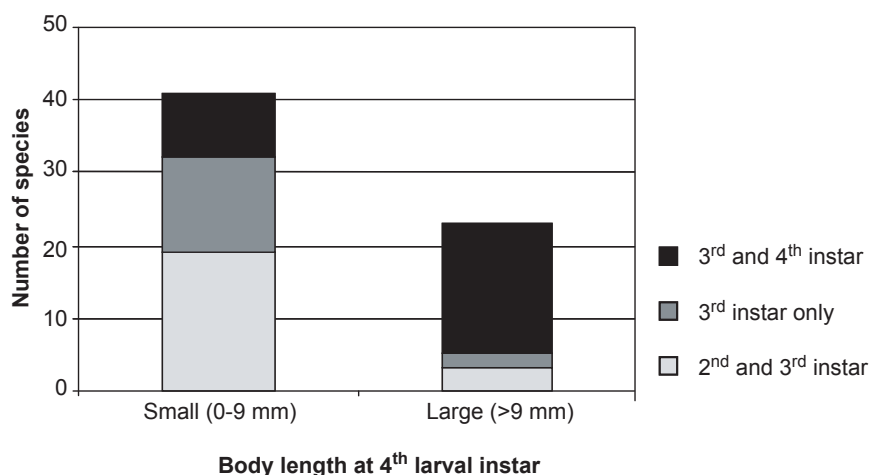**Figure 3** Differences in larval overwintering stage between small and large species of Chironomidae (based on unpublished data provided by Dr. H.K.M. Moller Pillot). White: species overwintering as 2nd instar and species overwintering both as 2nd and 3rd instar. Grey: species overwintering only as 3rd instar. Black: species overwintering both as 3rd and 4th instar and species overwintering only as 4th instar.

Table 2 Overview of the different life-history tactics, their most defining species traits and examples of typical species. Less defining species traits and species traits varying within a tactic are left blank.

	Tactics	Juvenile development	Period of juvenile development	Adult life span	Dispersal	Per capita investment	Synchronisation of juvenile development	Synchronisation of adult emergence	Voltinism	Tolerance to adverse abiotic conditions	Genetic recombination	Species examples
Dispersal	D1 short development time and strong dispersal	rapid		months-years	strong active dispersal			some				*Hydroglyphus pusillus* *Hesperocorixa sahlbergi* *Anopheles atroparves*
	D2 large clutch size and strong dispersal		long		strong active dispersal	low, large clutch size		yes	semi-univoltine			*Libellula depressa* *Chaoborus crystalinus*
	D3 early age at first reproduction and strong dispersal	rapid[1]	short				no	no	bi-multivoltine		low	*Gerris odontogaster* *Corynoneura scutellata* agg.
Synchronisation	S1 slow growth and synchronised emergence		long	weeks				yes				*Beraeodes minutus* *Procladius choreus*
	S2 short growth period and resistant stages	rapid					yes[4]	yes[4]	univoltine			*Aedes punctor* *Ilyibus guttiger, Lestes viridis* *Limnephilus luridus*
	S3 short synchronised juvenile development time	rapid		months-years			yes					*Agabus unguicularis* *Hydrophilus piceus*
	S4 high per capita investment, no active flight	rapid		months-years	no active dispersal	high	yes		univoltine			*Dugesia polychroa* *Glossiphonia complanata*
Developmental trade-off	T1 high tolerance, active dispersal	slow			low active dispersal		low			high		*Cognettia sphagnetorum*
	T2 high tolerance, no active flight	slow	long	months-years	no active dispersal		no	no		high	low	*Ceriagrion tenellum* *Peltodytes caesus* *Chaoborus pallidus* *Paratendipes* gr. *nudisquama*
Reproduction	R1 sequential reproduction, active dispersal	rapid		months-years		high[2]						*Hydrometra stagnorum* *Hydrobius fuscipes*
	R2 sequential reproduction with many small eggs, no active flight	slow		months	no active dispersal	moderate	some					*Erpobdella testacea* *Dendrocoelum lacteum*
	R3 sequential reproduction with parental care, no active flight	rapid		months	no active dispersal	high[2,3]	low		bi-multivoltine			*Asellus aquaticus* *Helobdella stagnalis*
	R4 early age at first reproduction, no active flight	rapid[1]	short		no active dispersal		no	no			low	*Tubifex tubifex* *Nais variabilis*

[1] Early age at first reproduction, [2] Protracted oviposition period, [3] Parental care, [4] Diapausing, resistant stages

Tactics

From the discussion above it is clear that species traits are interrelated both between and within different trait domains through functional combinations and trade-offs. Therefore, species traits cannot be viewed separately, but must be seen as an integral part of a complex adaptation, or life-history tactic. We have based our tactics on basic biological traits of species (shown in Fig. 1) and their interrelations known from life-history theory (summarized in the previous section). These interrelations can explain why high investments in one species trait constrain investments in another trait, or why investments in two species traits are coupled. As a result, when comparing various traits over different species, some traits may be more strongly developed or more pronounced compared to other traits. These within-trait differences loosely correspond to what Statzner *et al.* (1994) termed 'trait modalities'. As high investments in one trait constrain investments in another trait, such investments are most likely relevant to deal with a particular environmental problem.

Differences in investments over multiple traits can function to overcome different environmental problems. Theoretically, many different patterns of investment in species traits can be envisaged. Therefore, known patterns (represented by existing species) may be useful guides. Based on qualitative differences in such investment patterns we defined 13 life-history tactics (Table 2). Blank fields in the table indicate that a species trait is not defining for a given tactic. The trait is either not very pronounced in species assigned to that tactic, or investments may vary between these species.

Species assigned to the same life-history tactic are adapted to overcome a particular environmental constraint in a similar way. The actual traits to do so may differ. For example, to solve the problem of high egg mortality, similar types of solutions involving different investments in traits can be envisaged: endophytical oviposition, egg guarding, or ovovivipary. These solutions contrast with radically different types of solutions such as spreading egg mortality by laying more but smaller batches, or swamp egg predators by one massive synchronised reproduction event. These different types of solutions represent different tactics, which may present additional problems or present new opportunities. Therefore, a species' life-history tactic is the integrated response to all relevant environmental constraints.

This does not imply that all species found at a certain habitat patch will belong to the same tactic, or conversely that all species of a tactic are limited to a certain type of habitat. Rather, the combinations of tactics will be indicative for the functioning of a particular environmental situation. For example, different habitats (deeper waters with hypoxia during summer and shallow waters freezing completely in winter) may have in common a period of unsuitability. Species assigned to life-history tactic S2, which are able to deal with temporarily unsuitable conditions will be favoured in both habitats, although this tactic may be represented by different species in each habitat. Furthermore, tactics may represent a more extreme form of another (Fig. 4). For example, changes in the dominance of different species, resulting in a transition from tactic D3 to R1 to S1, would indicate a shift from unpredictable conditions to more predictable conditions, requiring less dispersal and more synchronisation. Furthermore, animals living in the same location may experience different levels of favourableness and constancy due to effects of scale and environmental heterogeneity (Southwood 1977), further resulting in different tactics coexisting in the same habitat.
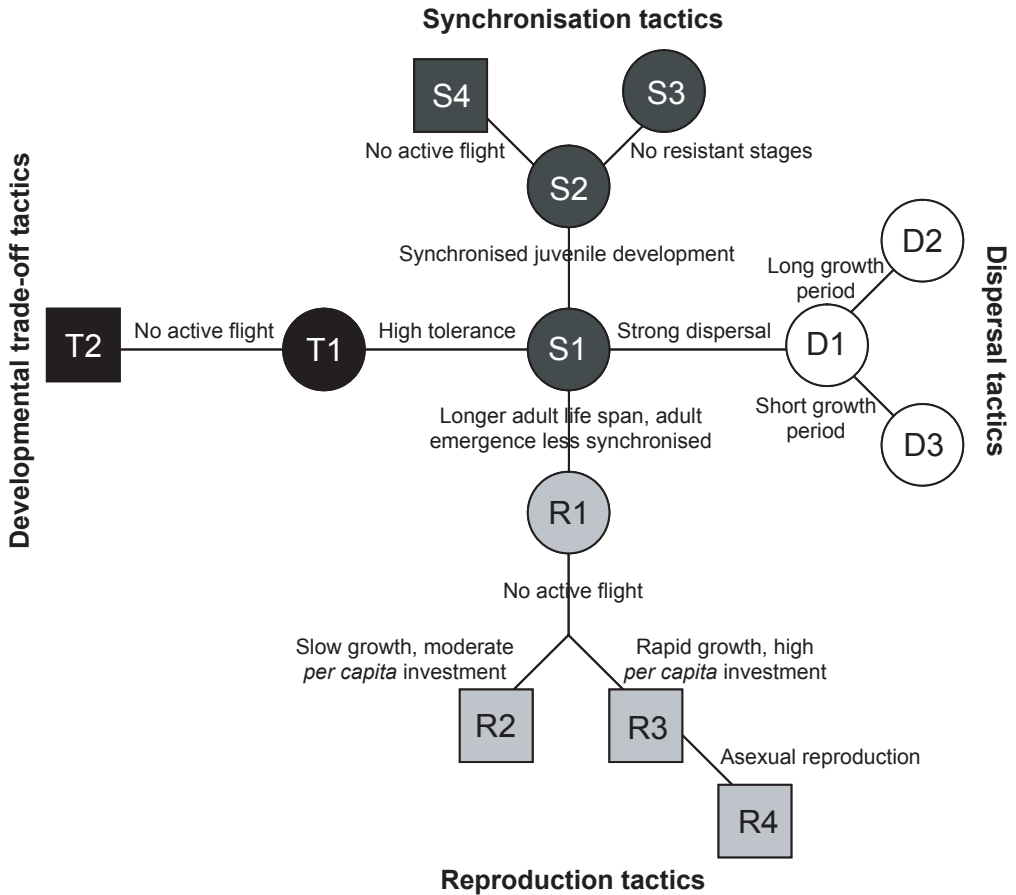
Figure 4 Overview of interrelationships between the different tactics defined for aquatic macroinvertebrates (see text for explanation). Table 2 shows species examples and defining species traits. Tactics with active dispersal are indicated with circles and those lacking active flight with squares.

Tactics are presented in four groups corresponding to the four domains (Fig. 4). Although species traits of all domains together shape a life-history tactic, certain combinations of species traits are more pronounced and therefore more defining for a given tactic. Life-history tactic S1 is placed centrally, as in this tactic most basic species traits are weakly pronounced, being defined by a long aquatic development period followed by a synchronized emergence of short-lived adults. For each tactic, the most defining combination of traits is given, in addition to species examples from several systematic groups (Table 2).

Dispersal tactics
Tactic D1: short development time and strong dispersal
Species in this tactic invest strongly in active flight capabilities and achieve a rapid development. The short development time and the high investments in flight (wing muscles and wings) constrain adult body size, investments in fat reserves, reproduction

capacity or a combination thereof. To circumvent this trade-off and generate sufficient energy for investment in reproduction, species have long-lived, feeding adults, which is combined with iteroparity and a high *per capita* investment.

Species examples include the dytiscid beetle *Hydroglyphus pusillus*, the waterbug *Hesperocorixa sahlbergi* and the mosquito *Anopheles atroparvus*. In each of these species, single eggs are deposited. *Hydroglyphus pusillus* is a good flyer (Verberk & Esselink 2005), ovipositing several times at different locations with a rapid larval development (6-8 weeks). *Hesperocorixa sahlbergi* is a monomorphic macroptere species with permanently developed flight muscles (Aukema *et al*. 2002), which enables this species to oviposit at different locations. *Anopheles atroparvus* has long-lived females which oviposit several times, with intermittent blood meals (Cranston *et al*. 1987). Because diapause in the egg stage is lacking, the winter period is passed as adults.

Tactic D2: large clutch size and strong dispersal

A large clutch size and strong dispersal are the main investments of species in this tactic. The large clutch size is related to a low *per capita* investment (semelparity) and a low investment in adult longevity. Low adult longevity and high dispersal may lead to problems associated with low densities, such as mating. To overcome this problem, species display a synchronisation of adult emergence.

Species examples include the dragonfly *Libellula depressa* and the phantom midge *Chaoborus crystallinus*. *Libellula depressa* has a high dispersal capacity and has a uni- or semivoltine life cycle. Females deposit numerous small eggs, clustered into small patches (Sternberg & Buchwald 1999). *Chaoborus crystallinus* is a semelparous uni-bivoltine species (Parma 1971) with a good dispersal capacity (Berendonk & Bonsall 2002).

Tactic D3: early age at first reproduction and strong dispersal

In addition to strong dispersal, species in this tactic have a high intrinsic rate of increase, which is achieved through multivoltinism, rather than a large clutch size. Rapid juvenile development is achieved at the cost of body size, adult longevity, dispersal, reproduction or a combination thereof. The rapid development and low adult longevity, decrease the age at first reproduction. Because synchronisation usually requires delaying juvenile development, it is poorly developed in this tactic,

Species examples include the semi-aquatic bug *Gerris odontogaster* and the chironomid midge *Corynoneura scutellata* agg. *Gerris odontogaster* is a small, dimorphic water strider. Microptere or macroptere morphs develop in response to environmental conditions (Vepsäläinen 1978), with a microptere summer generation giving rise to a mobile macroptere winter generation (Aukema *et al*. 2002). Microptere morphs are capable of a faster development, reflecting the trade-off between dispersal and development time (Vepsäläinen, 1978; Spence, 1989). *Corynoneura scutellata* agg. is a small, algivorous chironomid (4th instar larvae are 3½ mm). It's small clutch size (<100 eggs) reflects a trade-off between clutch size and development time. The high voltinism (up to 6 generations) compensates for the small clutch size as in multivoltine semelparous species (such as Chironomidae), the rate of increase is determined more by the age at first reproduction than clutch size (Stearns 1976). The species mainly reproduces asexually (H.K.M. Moller Pillot, personal communication), which circumvents the problem of finding mates that arises from the absence of synchronisation.

Synchronisation tactics

Tactic S1: slow growth and synchronised emergence

Species in this tactic have a strong synchronisation of adult emergence. This allows a low investment in adult longevity. Juveniles develop over a long period to achieve synchronisation. Investments in other adaptations do not stand out (*e.g.* clutch size and *per capita* investment, body size, tolerance of unfavourable conditions, dispersal).

Species examples include the caddisfly *Beraeodes minutes* and the chironomid midge *Procladius choreus*. *Beraeodes minutes* is a univoltine, detrivorous species with a short flight period in spring (Higler 2005). *Procladius choreus* is bivoltine and of intermediate size (4th instar larvae are 10 mm). The species has low haemoglobin levels and overwinters in the (near) final instar (H.K.M. Moller Pillot, personal communication), allowing a strong synchronisation of the spring generation.

Tactic S2: short growth period and resistant stages

Resistant stages enable species in this tactic to bridge long periods of unfavourable conditions, limiting time left for development. Juvenile development therefore proceeds rapidly and is synchronised to match favourable periods, effectively synchronising adult emergence. When eggs are the resistant stage, juvenile development is synchronised through egg diapause and when adults are the resistant stage, synchronised oviposition takes place. To ensure rapid juvenile development, species have a high *per capita* investment, which is combined with high adult longevity and (seasonal) iteroparity.

Species examples include the mosquito *Aedes punctor*, the damselfy *Lestes viridis*, the caddisfly *Limnephilus luridus* and the dytiscid beetle *Ilybius guttiger*. Both *Aedes punctor* and *Lestes viridis* survive unfavourable conditions as eggs, which are deposited singly and subsequently enter an obligate diapause (Cranston *et al.* 1987; Münchberg 1933). *Limnephilus luridus* has an adult diapause of 4-5 months and oviposition takes place in autumn after aestivation (Hiley 1978). *Ilybius guttiger* is seasonal iteroparous and their adults can also survive and hibernate on land, serving as resistant stages for both summer drought and winter frost. Oviposition takes place in autumn and larval growth is completed in early spring (Nilsson 1986).

Tactic S3: short synchronised juvenile development time

Juvenile development is short and synchronised, but in contrast to tactic S2, species in this tactic lack resistant stages. Long-lived, feeding adults solve the constraints involved with a short juvenile development time (see tactic D1). In contrast to tactic D1, investment in dispersal is low and species rather invest in egg size and egg protection (selective oviposition and brood care).

Species examples include the dytiscid beetle *Agabus unguicularis* and the hydrophilid beetle *Hydrophilus piceus*. *Agabus unguicularis* deposits eggs in leaf axils and larvae develop in spring. They have relatively broad head capsules, which enables the capture of larger prey and hence a rapid development in spring (Galewski 1971). Adults of *Hydrophilus piceus* can live up to 3 years and larvae develop rapidly in summer (within 4-6 weeks, Grabow 2000). Eggs are protected in a silk-woven cocoon.

Tactic S4: high *per capita* investment, no active flight

Species in this tactic lack active flight capabilities, which increases the importance of local persistence. Adult longevity is high and species have a high *per capita* investment. The

start of juvenile development is synchronised (to early spring) and the early phases of development proceed rapidly, giving juveniles a competitive advantage over other species.

Species examples include the triclad flatworm *Dugesia polychroa* and the leech *Glossiphonia complanata*. *Dugesia polychroa* produces large cocoons in April. These cocoons contain relatively few eggs (2.8 on average), which are provisioned with yolk (Reynoldson 1978). *Glossiphonia complanata* has relatively large eggs, which are guarded after deposition and hatch within 5-6 days (Dresscher & Higler 1982). Both yolk provisioning and egg guarding enhance survival of early juvenile stages. High mortality of later juvenile stages (Spelling & Young 1987) may promote seasonal iteroparity (Stearns 1976).

Developmental trade-off tactics
Tactic T1: high tolerance, active dispersal

The defining feature of species in this tactic is their high tolerance for unfavourable environmental conditions. Investments in physiological and morphological adaptations to combat this environmental hardship, constrain investments in reproduction, dispersal and body size. Consequently, species are small, have poor dispersal capabilities, a low reproduction capacity, or a combination thereof. Furthermore, juvenile development proceeds slowly and without strong synchronisation. Synchronisation of adult emergence may occur, but for non-environmental reasons such as mating or predator satiation.

Species examples include the damselfy *Ceriagrion tenellum*, the haliplid beetle *Peltodytes caesus*, the phantom midge *Chaoborus pallidus* and the chironomid midge *Paratendipes* gr. *nudisquama*. *Ceriagrion tenellum* is a semivoltine species (Buchwald 1994) despite being small and carnivorous. Larval development of *Peltodytes caesus* takes place in summer (van Vondel 1997) and larvae have tracheal gills, increasing their tolerance to periodic low oxygen levels. *Chaoborus pallidus* is a univoltine species, despite being small and carnivorous. In contrast, larger congeners such as *Chaoborus crystallinus* may complete two generations per year (Parma 1971). *Paratendipes* gr. *nudisquama* is very small (4th instar larvae are 4 mm long), has high levels of haemoglobin, and completes as little as two generations per year (H.K.M. Moller Pillot, personal communication).

Tactic T2: high tolerance, no active flight

This tactic presents a more extreme version of the previous tactic, with species lacking active flight capability altogether. Adult longevity is high and reproduction is mainly asexual. Juvenile development proceeds slowly and without synchronisation. Species can tolerate long periods of harsh conditions. Due to its constancy, innovations are not required, or may even prove maladaptive, and genetic recombination can be low.

A species example is the oligochaete *Cognettia sphagnetorum*. This species predominantly propagates asexually through architomy (fragmenting). Springett (1970) found regenerating fragments year round, with an increase in spring and summer. This mode of reproduction has a low degree of synchronisation, requires almost no preparation such as mating, building of fat reserves or cocoon production. Therefore when conditions are slightly more favourable, for instance when temperature or food availability increase, species can invest more in reproduction without depleting adults and jeopardising adult persistence.

Reproduction tactics

Tactic R1: sequential reproduction, active dispersal

A rapid juvenile development characterises species in this tactic. Nevertheless, juvenile development may take place over a long period, as the start of juvenile development is not synchronised, setting this tactic apart from tactic S2 or S3. Long-lived, feeding adults solve the constraints involved with a short juvenile development time (see tactic D1). In addition, adults have a protracted oviposition period, enabling them to feed in between oviposition, allowing a high *per capita* investment. The high *per capita* investment ensures the completion of juvenile development under harsh conditions or before the onset of harsh conditions and may confer competitive advantages by giving juveniles a head start. By spreading reproductive effort over a longer period, species minimize the chance of total reproductive failure.

Species examples include the semi-aquatic bug *Hydrometra stagnorum* and the hydrophilid beetle *Hydrobius fuscipes*. *Hydrometra stagnorum* has large eggs (1.7 mm long) and larval development can be completed within three weeks. Adults have a protracted oviposition period (Southwood & Leston 1959) with juveniles occurring from May to October (Aukema *et al.* 2002). *Hydrobius fuscipes* produces large cocoons (4 mm long) containing 15-20 eggs. Cocoon deposition takes place throughout spring and summer (J.G.M. Cuppen, personal communication). Larvae have large head capsules with long mandibles, which enables the capture of larger prey and hence a more rapid development.

Tactic R2: sequential reproduction with many small eggs, no active flight

Species in this tactic sequentially produce batches of eggs. Furthermore they invest in clutch size rather than egg size, which results in a longer development time, precluding offspring from reproducing in the same season. This tactic is intermediate to tactic R4 and S4, with juvenile development taking longer than in tactic R4 and being less synchronized than tactic S4. Species lack active flight capabilities and investment in adult longevity is low.

Species examples include the leech *Erpobdella testacea* and the triclad flatworm *Dendrocoelum lacteum*. In both species, adults successively produce a number of cocoons, after which they die (Dresscher & Higler 1982; Reynoldson 1978). The priority given to juvenile production over adult survival is also apparent from a study by Calow & Woollhead (1977) who showed that starving specimens of *D. lacteum* maintained high levels of reproductive effort, leading to shrinkage and high mortality of adults.

Tactic R3: sequential reproduction with parental care, no active flight

Similar to the previous tactic, species in this tactic spread reproductive effort over a longer period, lack active flight capabilities and have an adult life span of less than 1 year. Here species invest in egg size, rather than clutch size. The higher *per capita* investment is combined with parental care and allows a more rapid development. As a result, offspring may produce an additional generation in the same season.

Species examples include the isopod *Asellus aquaticus* and the leech *Helobdella stagnalis*. Both species continue to carry their offspring after hatching for several weeks. *Helobdella stagnalis* is even known to feed captured prey to their young (Kutschera & Wirtz 2001). A partial second generation may be produced in both species, with offspring from early spring reproducing later in the same year.

Tactic R4: early age at first reproduction, no active flight

Species in this tactic achieve a high rate of increase through early age at first reproduction, in combination with asexual reproduction (budding and apomictic thelytoky). A higher persistence compensates the lack of active flight capabilities, with species possessing species traits, such as cocoon formation and high levels of haemoglobin to deal with adverse environmental conditions. Intense competition is averted through environmental hardship, reducing the need for high genetic recombination (Siepel 1994) and parental care.

Species examples include the oligochaetes *Tubifex tubifex* and *Nais variabilis*. *Tubifex tubifex* can tolerate low oxygen levels, is capable of apomictic thelytoky (Baldo & Ferraguti 2005) and can complete several reproduction cycles per year with many descendents per cycle (Poddubnaya 1984). *Nais variabilis* can rapidly produce cocoons (Parish 1981) with the onset of adverse environmental conditions, which serve as resistant stages, while asexual reproduction through budding ensures high rates of increase.

Discussion

Templet theory (Southwood 1977) states that there is a match between species traits (combined in a species) and environmental conditions. Elucidating the match between traits and environmental conditions, is the key to explain differences in species assemblages between locations or periods. The problem lies in the huge range of species traits, making generalisations difficult (Townsend & Hildrew 1994). In this paper we have taken three steps to match species and environment through species traits. First, we have identified environmental key factors by combining and extending the ideas of Southwood (1977) and Stearns (1976), and derived which species traits are relevant in dealing with these key factors. Second, we investigated how investments in species traits are interrelated in aquatic macroinvertebrates. Third, we outlined various life-history tactics, based on the interrelations between traits and their functional implications. Life-history tactics represent different solutions to particular ecological problems, thus providing a connection between species traits and environmental conditions. Species assigned to the same life-history tactic have similar functional relations to their environment. The actual traits possessed by species may differ, as species may originate from different systematic groups and differ in basic morphology. Nevertheless, the different traits solve problems for a species' survival in a similar way.

Previous studies have used multivariate analysis techniques to make sense of the diversity in species traits (*e.g.* van Kleef *et al.* 2006; Ilg & Castella 2006). In these studies, species traits, species and sites have been analysed to determine how species traits shape species-environment relations. A bold attempt to link species to their preferred habitat through species traits was made for species in the riverine landscape of the Rhône river (Statzner *et al.* 1994). Although different species may largely behave as independent units, different traits are firmly linked within species. They recognised this by first analysing species-species traits relations and species-environment relations separately and subsequently link both analyses through co-inertia analysis (Dolédec & Chessel 1994). However, such analyses weight traits equally (independent from other traits possessed) across different taxa and consequently result in clusters of taxa largely corresponding to systematic units (*e.g.* Usseglio-Polatera *et al.* 2000). While systematic units differentiate to some extent, these clusters provide insufficient resolution to characterise differences in

invertebrate assemblages between water bodies, where many species belonging to different systematic units co-occur. In a synthesis of their work on habitat templets in the Rhône river, Resh *et al.* (1994) conclude that their analyses supported few a priori predictions, for which they give five reasons; '…templet theories do not yet accommodate (i) alternative suites of characteristics, and (ii) trade-offs between combinations of traits, or perhaps … (iii) the single scale of variability considered in the analyses, (iv) the inhomogeneity of the available biological information, and (v) the aggregation of species traits that were used created methodological problems…'.

The life-history tactic approach tackles or circumvents each of the five difficulties of the multivariate approach mentioned above. By explicitly taking interrelations between species traits into account (ii), the adaptive value of separate traits is no longer equal, but depends on their adaptive value as a part of the species' biology (Gould & Lewontin 1979). For example, feeding guild and body size are traditionally viewed as important aspects of a species' biology (Cummins 1973; Calder 1984). In isolation, feeding guild and body size are not decisive in assigning species to a tactic, but they gain relevance when placed within the context of the other species traits, setting limits to development speed, shaping a species' tactic indirectly, for example through relations with voltinism, adult life time and degree of synchronisation. Difficulties with the method of aggregation (v) and the possibility of 'alternative suites of characteristics' (i) were tackled by grouping alternative trait combinations into the same tactic when they solve an environmental problem in a similar way By taking into account species traits such as life span, mobility and body size (governing the relevant scale level from an animal's perspective), different scales in variability (iii) are covered. Although not solved, the problem of inhomogeneity of available biological information (iv) is circumvented. Recognising that taxon specific traits function to solve a particular environmental problem, allows a (qualitative) comparison spanning different systematic groups (Table 1).

Phylogeny is intrinsically linked to attempts to generalize the diversity in species traits, as interspecific differences in traits may reflect different evolutionary pathways, rather than solutions to particular ecological problems (Gould & Lewontin 1979; Townsend & Hildrew 1994). This recognition has led several authors to emphasise the need to correct for phylogenetic relatedness in order to arrive at statistically independent contrasts (Felsenstein 1985; Reynolds & Lee 1996; Poff *et al.* 2006). In this way, information on the co-variation between species traits and phylogenetic structure is discarded to comply to statistical assumptions. In contrast, this information is incorporated in life-history tactics for two reasons.

First, observed differences in species traits may be functionally similar: species may possess different combinations of species traits due to differences in basic morphology, but different trait combinations can solve the same environmental problem (Felsenstein 1985; Koehl 1996). One example is the protection of egg stages, which can be achieved through endophytical oviposition (*e.g. Aeshna cyanea*), a gelatinous matrix (*e.g.* the caddisfly *Limnephilus luridus*) or ovoviviparity (*e.g.* the mayfly *Cloeon dipterum*). Another example is increasing the chance of locating a mate for copulation. This can be achieved by synchronising adult emergence (*e.g.* the dragonfly *Leucorrhinnia dubia*), but other solutions are extending adult life time (*e.g.* the hydrophilid beetle *Hydrophilus piceus*), or -more drastically- abandoning sexual reproduction altogether (*e.g.* the chironomid midge *Corynoneura scutellata* agg.).

Second, information on a species' phylogenetic structure reveals constraints set by their basic morphology, which may help in deriving the functional implication of trait combinations. For example, adults of the mayfly *Cloeon dipterum* are short-lived, do not feed and resources are allocated mainly to egg production. Investment in adult body structures is minimal, precluding the development of a sclerotized ovipositor. Therefore, ovoviviparity in *Cloeon dipterum* most likely serves as an alternative solution for egg protection. such as ovoviviparty. A different example where the phylogenetic history reveals a constraint rooted in a species' basic morphology is the difference in cocoon formation in Hirudinea. The formation of cocoons, among others, reflects their ancestral origin in the Oligochaeta (Siddal & Burreson 1996). It functions as a resistant stage in many species of Oligochaeta, but cocoons are vulnerable to predation by snails (Kutschera & Wirtz 2001). Species have countered that problem by developing parental care (*e.g.* the leech *Alboglossiphonia heteroclita*) or by depositing their eggs terrestrial (*e.g.* the leech *Haemopsis sanguisuga*). This opened the way to inhabit snail dominated habitats, where -ironically- snails now form the major food component of their diet. In conclusion, differences in species traits between systematic groups either related to phylogeny or not, were translated to functional differences and similarities.

Our paper is an attempt at a coherent synthesis of biological differences between aquatic macroinvertebrates through a functional interpretation. We have defined life-history tactics, based on the relations between traits and their functional implications, to better understand how species are linked to their environment. A life-history tactic can be considered an integrated response to all relevant environmental conditions. Studying the distribution of species numbers over the various life-history tactics in a location thus gives direct information about how a particular environment is experienced by the species present. Life-history tactics may therefore constitute a promising tool to explain differences in species assemblages between locations or periods. As such it may be widely applicable from ecological research to environmental quality assessment programmes (Chapter 4).

Grouping species with similar functional relationships into tactics may allow a comparison of water bodies found at a large geographical distance, which may comprise different regional species pools or span species distribution areas (Mouillot *et al.* 2006). The use of life-history tactics increases the signal to noise ratio, reducing often very complex, biodiverse assemblages into a few meaningful, easily interpretable relationships (Steneck & Dethier 1994).

A drawback of a more practical nature is that considerable biological knowledge at the species level is required, in addition to consistent identification to species level, as it proves difficult to generalise to genera or higher taxa. However, we have shown that species traits are strongly interlinked. Therefore, exhaustive data on every aspect of a species' biology does not seem necessary. Rather information on a number of key traits is sufficient to assign a species to a certain tactic. This information can be used to guide future research to fill specific gaps in knowledge of a species' biology.

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One of the sampled water bodies in the Korenburgerveen reserve on 15 September 2004. This ditch, "de Brandsloot", was dug in the time of steam locomotives to obtain a ready supply of water to extinguish fires. It now harbours one of the largest populations of the threatened northern damselfly (Coenagrion hastulatum). Photo: Wilco Verberk.

Chapter 4

Applying life-history tactics for freshwater macroinvertebrates to lentic waters

Verberk WCEP, H Siepel & H Esselink

Summary

Effective nature management requires a sound understanding of the causal mechanisms underlying the relationship of species with their environment. Mechanistic explanations linking species and environment are ultimately based on species traits. Many tools for ecological assessment and biomonitoring lack such explanations. Elsewhere, we have defined life-history tactics, based on the relations between species traits and their functional implications. Life-history tactics represent different solutions to particular ecological problems, thus connecting species and their environment through species traits.

This study tests the hypothesis that life-history tactics can provide insight in how different water types function for aquatic macroinvertebrates. Life-history tactics were used to analyse data on aquatic macroinvertebrates in a variety of water bodies, which differed in environmental conditions and were therefore expected to function differently for aquatic macroinvertebrates.

Results show clear differences in tactic composition between the different water types, which could be related to the prevailing environmental conditions through mechanistic explanations.

By reducing diverse species assemblages to a small number of tactics, representing easily interpretable relationships, this approach may be useful in environmental quality assessment programs, including those required by the European Water Framework Directive.

Based on mechanistic explanations, life-history tactics may generate testable predictions and guide future research. Recognising the general patterns in species assemblages allows us to see and focus on the exceptions. These exceptions are the driving force behind advances in our knowledge.

Introduction

For the use of macroinvertebrates in ecological assessment and biomonitoring, water managers have a wide variety of tools at their disposal (Verdonschot 2000). These tools range from simple indices, such as diversity indices, EPT-taxa richness, or the *Gammarus-Asellus* ratio to more advanced and complex methods such as multimetrics or multivariate analysis techniques (*e.g.* Whitehurst 1991; Wallace *et al.* 1996; Thorne & Williams 1997; Chessman 1999). Vital for the effectiveness of management is a clear understanding of the functioning of the system of interest and changes therein due to anthropogenic impacts. The above methods or calculation tools may generate testable predictions (Verdonschot 2000), but do not give scientific understanding, which ultimately comes from mechanistic explanations (Weiner 1995). In addition, the complex methods used in ecological assessment and biomonitoring may lead to different conclusions, depending on subjective choices made during the data analysis (Nijboer 2006). Linking species and environment to explain patterns in species occurrence in space and time is fundamental in ecology for both practical and theoretical questions (Townsend & Hildrew 1994).

There is broad consensus that the way forward is to link pattern and process through species traits (*e.g.* Keddy 1992; McGill *et al.* 2006). Many studies have incorporated species traits in multivariate analysis techniques to explain differences in species occurrence between locations or periods (Resh *et al.* 1994; van Kleef *et al.* 2006; Bremner *et al.* 2006). In such analyses traits are treated as equivalent and unrelated units, while in fact traits are strongly interrelated through functional combinations and trade-offs and their indicative

value depends on their adaptive value as a part of the entire organism's biology (Gould & Lewontin 1979; Chapter 3). An additional problem is that alternative trait combinations may be functionally equivalent (Resh *et al.* 1994; Chapter 3). Elsewhere, we have attempted to solve these problems by defining life-history tactics for aquatic macroinvertebrates (Chapter 3). Stearns (1976) defines a life-history tactic as 'a set of co-adapted traits designed, by natural selection, to solve particular ecological problems'. In life-history tactics, interrelations between species traits are taken into account and species trait combinations are grouped based on their function. Life history tactics can therefore be seen as an integrated response to the environment.

In this study we test whether these theoretically derived life-history tactics can provide insight in the functioning of existent water types for aquatic macroinvertebrates. Therefore, we apply life-history tactics to previously gathered data on various water bodies belonging to different water types. These water types differ in species assemblages and environmental conditions (Chapter 2) and are therefore expected to function differently.

Methods

Study area and invertebrate sampling
The study was conducted in the nature reserve Korenburgerveen in the Netherlands (N: 51°59'; E 6°39'; 310 ha). The Korenburgerveen consists of a raised bog centre surrounded by more minerotrophic parts, with several environmental gradients in between. In total, 45 water bodies were sampled. 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.

Macroinvertebrates were collected using a standard 30 x 20 cm pond net with a mesh size of 0.5 mm. Samples consisted of a sweep starting from the substrate and from more or less open water into denser vegetation near the shore. Samples were sorted in the laboratory. Tricladida, Hirudinea, Oligochaeta, Araneae, Crustacea, Megaloptera, Odonata, Hemiptera (adults and nymphs), Coleoptera (adults and larvae), Cylindrotomidae, Chaoboridae, Dixidae, Culicidae, Chironomidae and Trichoptera were identified to species level and used in the analysis.

Based on differences in environmental conditions (nutrient concentrations, acidity, alkalinity, soil type, dimensions, degree of shading and vegetation composition), the water bodies were classified into three main water types and eight subtypes. Average values for different physical and chemical properties of the subtypes are listed in table 1. Further details on the study area, sampling method and typology are given in Chapter 2.

Tactic assignment and data analysis
All 238 taxa collected were assigned to a life-history tactic based on their species traits (see table 2 for species traits defining tactics, see Appendix 1 for taxon names and their assignment). Information on a species' basic biological traits was retrieved from a range of literature and supplemented by experts. For each water body sampled, the abundance of each species was expressed as a percentage of the total number of individuals. When a water body was sampled in both spring and autumn, the percentages from both sampling rounds were averaged. Taxa belonging to the same tactic were pooled.

Table 1 Differences in physical and chemical conditions between the different water types. Averages ± standard error are shown.

Main type	Water type	# 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[1]
Mesotrophic waters	shallow mesotrophic puddles	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
	large mesotrophic pools	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	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
Water bodies in wet forests	water bodies in *Salix-Betula* forests	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	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
Bog pools	large bog pools	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	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	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

[1]Indicating the proneness to dessication of a water body, ranging from 0 (permanent) to 1 (temporary)

Table 2 Overview of the different life history tactics and their most defining species traits. Less defining species traits and species traits varying within a tactic are left blank.

Tactics		Juvenile development	Period of juvenile development	Adult life span	Dispersal	*Per capita* investment	Synchronisation of juvenile development	Synchronisation of adult emergence	Voltinism	Tolerance to adverse abiotic conditions	Genetic recombination
Dispersal	D1	rapid		months-years	strong active dispersal			some			
	D2		long		strong active dispersal	low, large clutch size		yes	semi-univoltine		
	D3	rapid[1]	short				no	no	bi-multivoltine		low
Synchronisation	S1		long	weeks				yes			
	S2	rapid					yes[4]	yes[4]	univoltine		
	S3	rapid		months-years			yes				
	S4	rapid		months-years	no active dispersal	high	yes		univoltine		
Developmental trade-off	T1	slow			low active dispersal		low			high	
	T2	slow	long	months-years	no active dispersal		no			high	low
Reproduction	R1	rapid		months-years		high[2]					
	R2	slow		months	no active dispersal	moderate	some				
	R3	rapid		months	no active dispersal	high[2,3]	low		bi-multivoltine		
	R4	rapid[1]	short		no active dispersal		no	no			low

[1] Early age at first reproduction, [2] Protracted oviposition period, [3] Parental care, [4] Diapausing, resistant stages

Differences in the tactics (summed percentages) were statistically tested for the three main water types, but not for the eight subtypes, due to low number of replicate water bodies within subtypes. For each tactic, differences in the proportion of a tactic (percentage) between the three main types were tested non-parametrically using a Kruskal-Wallis test.

Results

Most tactics were represented by species from different systematic groups and different tactics were represented within a systematic group (Table 3). Tactics S4 R2, R3, R4 and T2 occurred mainly in non-insect groups, including leeches, worms and triclads, reflecting differences in their basic morphology. These groups lack active flight and have a hermaphroditic and asexual reproduction. In insects, the number of species representing the various tactics differed between the systematic groups, but without consistent differences between for example holometabolous and hemimetabolous insects. Species assigned to tactics D1, S2, S3, R1 and T1 belonged to systematic groups with many aquatic species (Diptera, Coleoptera, Odonata, Hemiptera and Trichoptera; Table 3) and consequently these tactics were represented by many species (Fig. 1). Relative to the

number of species, tactics with a -potentially- high intrinsic rate of increase due to short generation time or hermaphroditic or asexual reproduction (tactics R3, R4 and T2) were strongly represented numerically (Fig. 1).

Table 3 Number of species in a systematic group and their distribution over the life-history tactics. The number of life-history tactics for each systematic group is indicated between brackets. Taxon names are given in appendix 1.

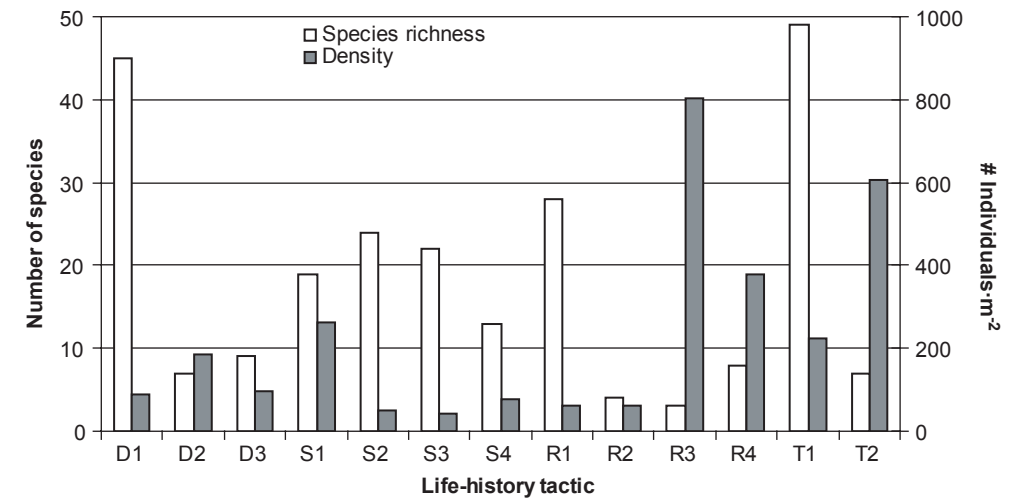| Systematic group	Total	T2	T1	R3	R2	R1	R4	D3	D2	D1	S4	S3	S2	S1
Tricladida	4 (2)				2						2			
Hirudinea	6 (3)			2	2						2			
Oligochaeta	23 (3)	6					8				9			
Odonata	15 (4)		6					3					4	2
Ephemeroptera	1 (1)								1					
Hemiptera	20 (4)		4			7			3	6				
Coleoptera	86 (7)	1	12			19				23		22	7	2
Diptera	64 (6)		19			2		9		15			6	13
Trichoptera	15 (4)		5							1			7	2
Arachnida	1 (1)		1											
Crustacea	1 (1)			1										
Plecoptera	1 (1)		1											
Megaloptera	1 (1)		1											
Total	238	7	49	3	4	28	8	12	4	45	13	22	24	19

Figure 1 Species richness (number of species) and species density (# individuals·m^{-2}) for each life-history tactic. Average densities were calculated for each species and subsequently averaged for species in the same tactic.

The percentual composition of the tactics differed strongly between the eight different subtypes in the study area (Fig. 2). Also when subtypes were aggregated, significant differences between the three main water types were found for eight tactics (Fig. 3).

The shallow mesotrophic puddles were acid and susceptible to fluctuations in water level, but were unlikely to dry out completely. Species with a high tolerance for unfavourable conditions (tactic T1) and without active dispersal (tactics R3, R4 and T2)
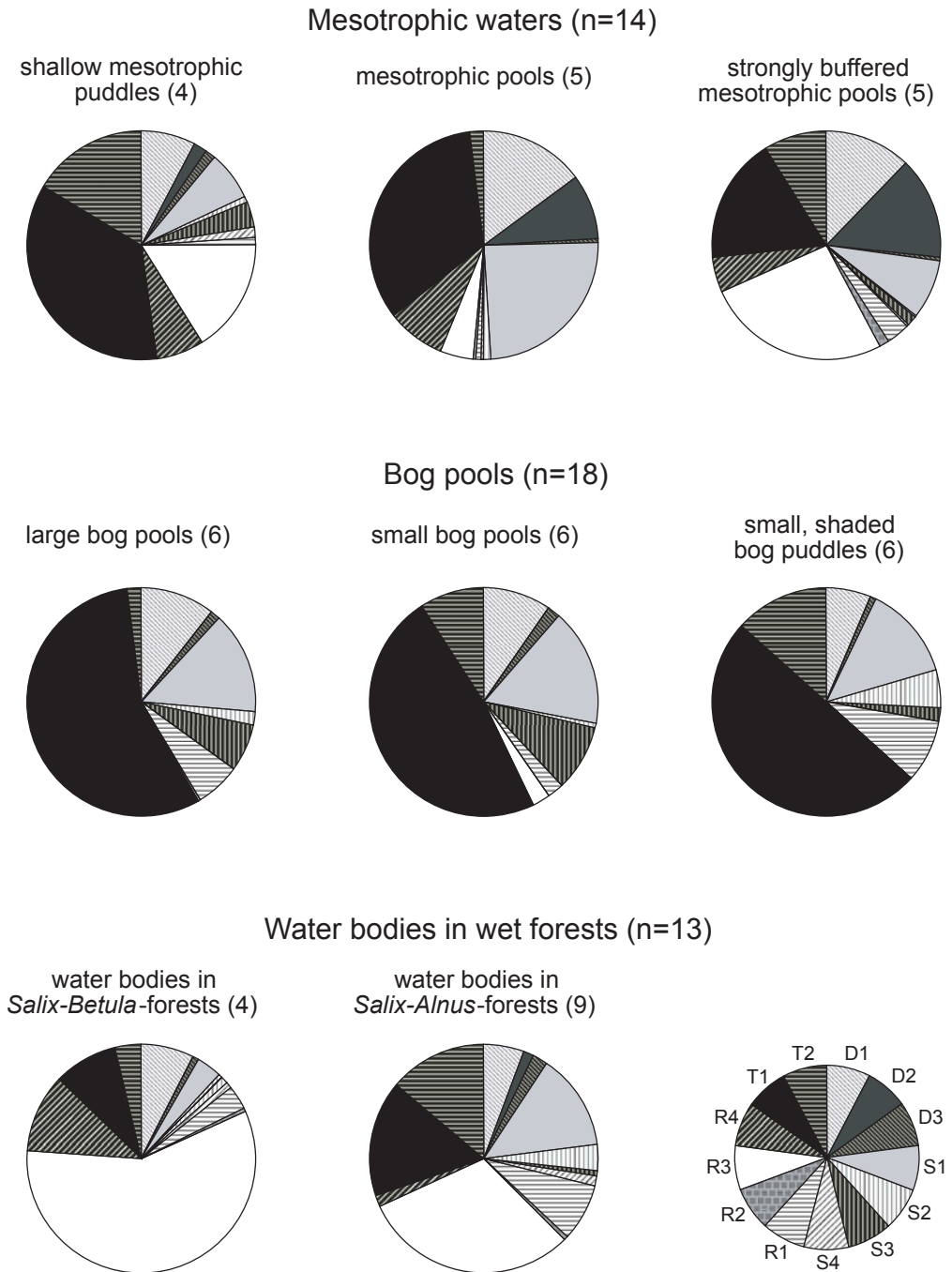
Mesotrophic waters (n=14)

shallow mesotrophic
puddles (4)

mesotrophic pools (5)

strongly buffered
mesotrophic pools (5)

Bog pools (n=18)

large bog pools (6)

small bog pools (6)

small, shaded
bog puddles (6)

Water bodies in wet forests (n=13)

water bodies in
Salix-Betula-forests (4)

water bodies in
Salix-Alnus-forests (9)

T2 D1
T1   D2
R4   D3
R3   S1
R2   S2
R1   S3
S4

Figure 2 Proportion of life-history tactics in each of the eight water subtypes. Percentages are averaged for
water bodies of the same type. The number of water bodies is given between brackets.
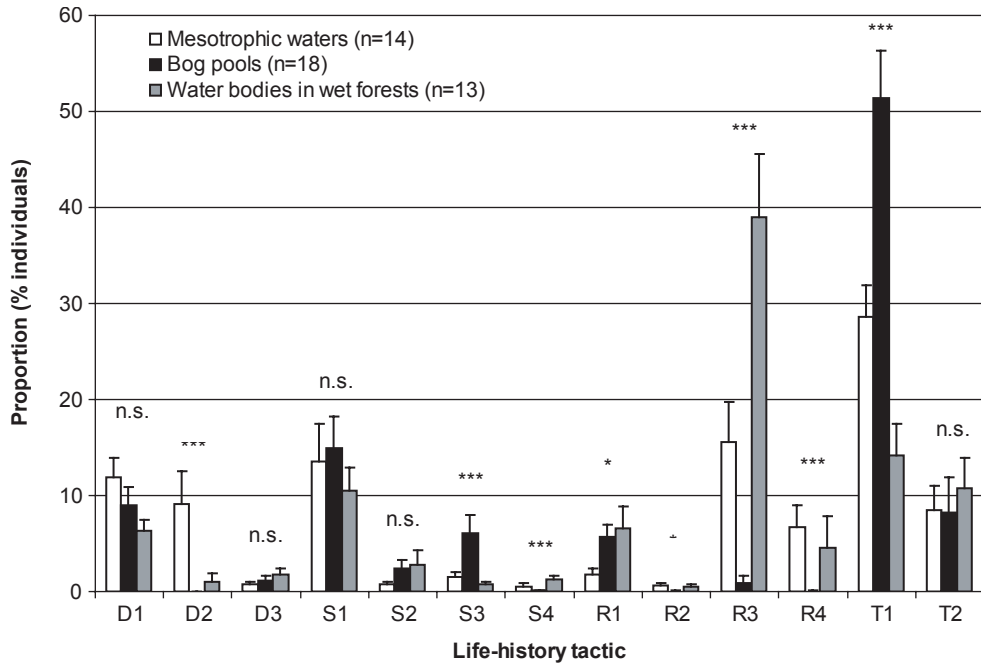
Figure 3 Proportion of life-history tactics (expressed as percentages ± standard error) in each of the three main water types. Percentages are averaged for water bodies of the same water type. The number of water bodies is given between brackets. Asterisks indicate significant differences (Kruskal-Wallis test): n.s.: $P>0.05$; *: $P<0.05$; ***: $P<0.001$.

were most abundant. These latter tactics compensate their low dispersal capacity by a high persistence, in combination with a -potentially- high intrinsic rate of increase through hermaphroditic and asexual reproduction. Species in tactic T2 are very tolerant to harsh conditions and are therefore expected to reach high abundance under very different conditions than species in tactic R4. Species in tactic R4 maximise their rate of increase through minimising their age at first reproduction, which works best under more productive conditions. The high abundance of both tactics indicates that environmental conditions have fluctuated. This corresponds to the field situation, as nutrient rich surface water occasionally flowed into the area where the water bodies were located. In addition, these water bodies were located on permeable soils and may have alternated between seepage and infiltration as a result from seasonal fluctuations in ground water influence.

Mesotrophic pools were large, sun exposed water bodies, which represented a very stable and benign environment (no food shortage, low acidity, high oxygen). This is reflected in the high abundance of species with a long period of juvenile development and a synchronised emergence of short-lived adults (tactic S1), and a low abundance of species of tactic R3, which perform best under more unpredictable conditions. Species following a resource dominance strategy through a high clutch size (tactic D2) or asexual reproduction (tactic R4) were also abundant in mesotrophic pools.

Strongly buffered mesotrophic pools were more shaded, eutrophic and smaller compared to the mesotrophic pools. In addition they were shallower making them more susceptible to drying out. In addition, conditions were less stable, but more productive. This explains the high abundance of species following a resource dominance strategy,

including species from tactic D2 and R4, but also species from R3. Species adapted to more stable conditions (tactic S1) were less abundant. Permanently unfavourable conditions such as high acidity or low conductivity were absent here, explaining the low abundance of species with a high tolerance for such unfavourable conditions (tactic T1).

Water bodies in forests were most variable in terms of periodic drought. Water bodies in *Salix-Betula* forests were most susceptible to drying out, but the soil will have remained moist as the water bodies were located on peat moss soils. These water bodies thus represented fluctuating conditions, without becoming completely unsuitable. Under these conditions, species that have a fast development and spread successive reproduction attempts over a longer time period (tactic R3) are most successful.

Water bodies in *Salix-Alnus* forests were richer in nutrients and had more seepage. In water bodies that did not dry out, species from tactic S1 were abundant, while species of tactic R3 were less abundant. Other water bodies in *Salix-Alnus* forests did dry out, and here the occurrence of drought was more predictable and complete, compared to the water bodies in *Salix-Betula* forest. This is reflected in the higher abundance of species with a short synchronised juvenile development and resistant stages (tactic S2). A higher abundance was also achieved by species with a rapid juvenile development spread over a long period (tactic R1). Although similar to tactic R3 in a number of ways, species in this tactic have long lived adults capable of dispersal, enabling them to survive the dry period elsewhere.

Bog pools were most acidic compared to the other water types (Table 1) and represented a harsh but predictable environment. Species with a high tolerance for unfavourable environmental conditions (tactic T1), and species with a slow and synchronised juvenile development (tactic S1) were most abundant. Within bog pools the three subtypes differed in size, degree of shading and susceptibility to drying out. Tactic composition was very similar between the different subtypes, with a high percentage of tactic T1, although this tactic was represented by different species in the various subtypes (Fig. 4). Large bog pools show high abundance of *Ceriagrion tenellum* and *Argyroneta aquatica*, while small, shaded bog puddles showed high densities of *Polypedilum uncinatum* agg. and *Cyphon* sp. In small shaded bog puddles drought may have been more complete, due to their smaller size. This may explain the higher abundance of species of tactic S2 in small shaded bog puddles, while species of tactic S3 were more abundant in the other types of bog pools. Both tactics have a short and synchronised juvenile development allowing them to make use of predictable favourable periods, but in contrast to tactic S2, species in tactic S3 lack resistant stages and are therefore less capable of bridging completely unfavourable periods.

Discussion

Our results demonstrate that life-history tactics provide a functional classification of macroinvertebrates spanning across the different systematic groups (Table 3). In our analyses we focussed on species abundance rather than species richness. The rationale behind this is that an ecological successful tactic will be represented by many individuals, whereas an evolutionary successful tactic will be represented by many species. Indeed, differences in tactic composition based on number of individuals (Fig. 1), reflected characteristics of the tactics, such as intrinsic rate of increase. Conversely, differences based on number of species reflected phylogeny with some tactics represented largely by
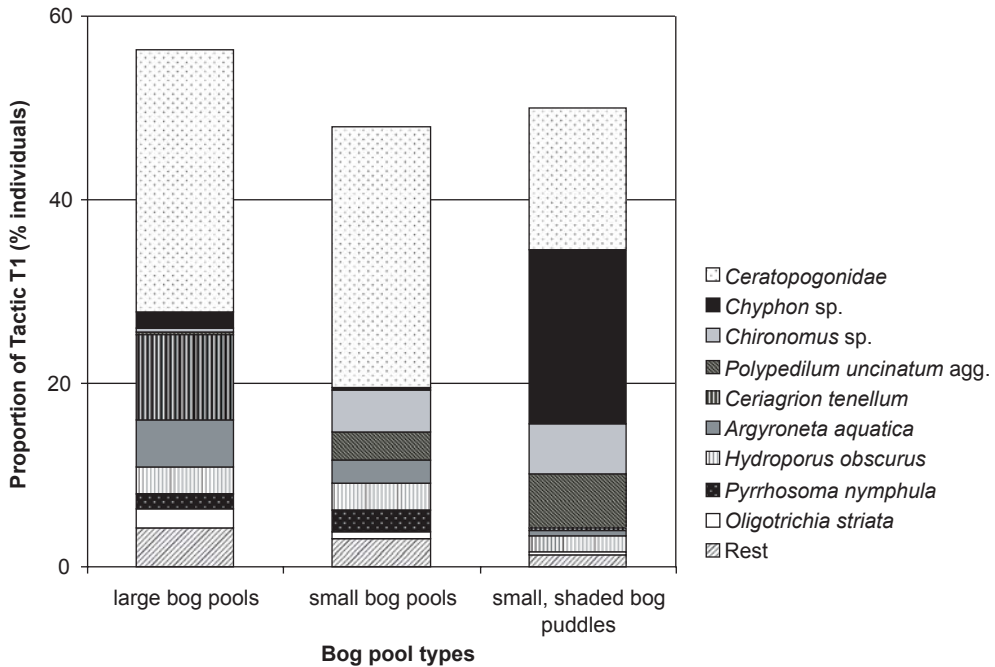
Figure 4 Proportion of life-history tactic T1 in the bog pools, showing the nine most abundant taxa separately.

speciose groups such as Diptera and Coleoptera. This makes individuals a more straightforward unit than species, supporting our supposition to base analyses on individuals.

Different species have different species traits but may be grouped into the same life-history tactic, provided that the combination of species traits solve problems for a species' survival in a similar way. For example, a high percentage of individuals belonging to tactic T1 was found in each type of bog pool (Fig. 2), despite large variation in the abundance of individual species, which belonged to different systematic groups (Fig. 4).

By pooling species of the same tactic, the major differences between the function of the different water types for aquatic macroinvertebrates are brought into focus. In addition, species identity is made subordinate to how they are adapted to various environmental conditions. This allows a functional comparison of water bodies found at a large geographical distance, which may comprise different regional species pools (Keddy 1992) or span species distribution areas (Mouillot *et al.* 2006).

In this study, we related differences in tactic composition between the different water types to the prevailing environmental conditions governing the predictability and variation of habitat suitability in space and time. In this way we have provided plausible links between two data-sets of different origin, with on the one hand data from literature on the biology of the various species (condensed in life-history tactics, see Chapter 3) and on the other hand field data on both species occurrences and environmental conditions (described in Chapter 2). This demonstrates the value of life-history tactics in providing mechanistic explanations for differences in species assemblages.

The relation between tactic composition and ecosystem functioning provides an advantage to more traditional assessment methods, which have less straightforward relations to ecosystem functioning (Mouillot *et al.* 2006). For example, relationships between simple indices (such as species richness) and ecosystem processes (such as disturbance and productivity) are equivocal due to non-linearity (Huston 1979; Grime 1977) and may vary with scale (Chase & Leibold 2002). Rapid assessments using multivariate analysis techniques and assessments employing multimetrics are usually not related *a priori* to ecosystems functioning. Rather, the complex patterns in environmental conditions, species occurrences and species traits are described *a posteriori* (Usseglio Polatera *et al.* 2000; Ilg & Castella 2006). Linking these complex patterns to ecosystem function and impairment thereof, involves equally complex descriptions of reference conditions, which are used for calibration (Reynoldson *et al.* 1997; Chessman 1999; Bates Prins & Smith 2007). Thus, in simple indices too few information is taken into account or remains after aggregating complex information into single indices. In contrast, in more advanced and complex methods too much information is generated, resulting from a failure to identify key mechanistic explanations underpinning patterns in species occurrence. Life-history tactics offer a suitable middle way. Applying life-history tactics reduces the vast complexity of many species belonging to many different systematic groups to a small number of tactics (although species identification will remain necessary). These tactics have functional relations to the duration, degree and predictability of habitat suitability in space and time. Our results show that the identity of the tactics, their numerical dominance and their co-occurrence with other tactics can provide insight in how the environment functions for the species present.

Within a Driver-Pressure-State-Impact-Response (DPSIR) framework, such as used within the EU water framework directive (IMPRESS 2003), life-history tactics may be useful in interpreting documented changes in state or impact. This allows significant pressures to be identified and (cost-)effective responses to be undertaken. Based on mechanistic explanations, life-history tactics are not restricted to interpolation within the parameter space on which the calibration was performed, but can make predictions over a much wider range of conditions (Weiner 1995). The need to go beyond interpolation will become increasingly important, as human impacts continually create new situations. These may involve new environmental conditions. For example, eutrophication of raised bogs (van Duinen *et al.* 2006) has resulted in the combination of high acidity and high nutrient availability. In the historical situation, these two conditions were mutually exclusive. Additionally, human activities, such as interconnecting river basins through man-made canals, may facilitate the invasion of species into regions where they were historically absent (bij de Vaate *et al.* 2002). As these species possess new trait combinations, they may have a large impact on ecosystem functioning. New environmental conditions often facilitate species invasions, which is documented for eutrophication (Chase & Knight 2006), disturbance regime (Hobbs & Huenneke 1992) or changes in conditions creating niche opportunities in general (Shea & Chesson 2002).

Life-history tactics may generate testable predictions and guide future research. For example, species in tactic D1, D2, D3, R3 and R4 are predicted to play a minor role in the functioning of stable systems, while in unpredictable and dynamic systems they will play a crucial role. A study on mosquito's in wetlands by Chase & Knight (2003) supports this prediction. They showed that *Culex pipiens* and *Anopheles quadrimaculatus,* which can both be assigned to tactic D1, performed best in semi-permanent water bodies where the

occurrence of drought was unpredictable. Future research may provide new insights on a species' biology and may lead to a rearrangement of that species in a different tactic. Likewise, extending our approach to all freshwater ecosystems, and incorporating other systematic groups (*e.g.* fish, plants, zooplankton) may reveal new life-history tactics. Recognising the general patterns in species assemblages allows us to see and focus on the exceptions, which lead to new insights, improving our knowledge.

Acknowledgements

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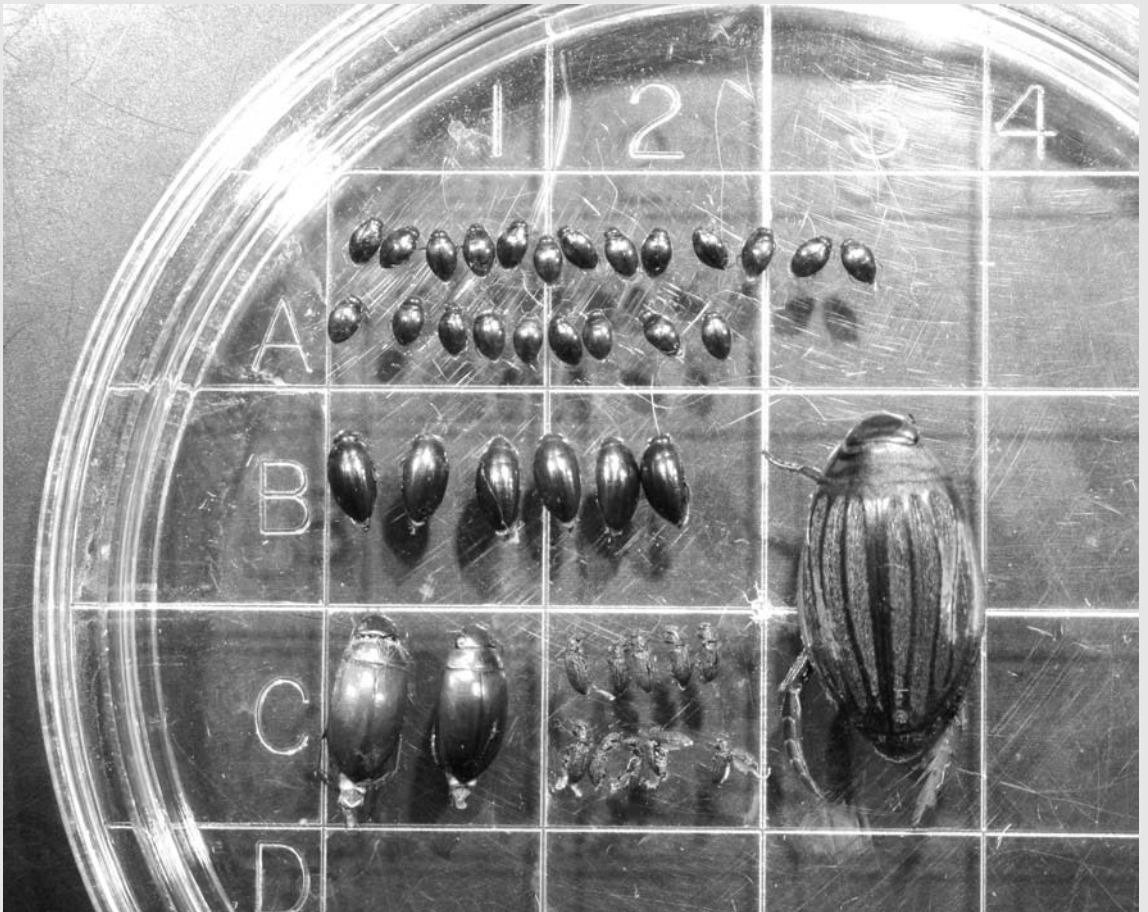
Impression of species identification in the lab. Different species of water beetles are shown: Hygrotus decoratus (A1-A3), Noterus crassicornis(B1-B2), Copelatus haemorrhoidalis (C1), Acilius canaliculatus (B3, C3) and Hydrochus carinatus (C2). Photo: Wilco Verberk

Species traits and niche breadth in aquatic macroinvertebrates: disentangling the various explanations for interspecific abundance-occupancy relationships

Verberk WCEP, G van der Velde & H Esselink

Summary

A positive interspecific abundance-occupancy relationship is one of the most robust patterns in macroecology, for which various explanations have been proposed. To disentangle the various explanations we analysed how a species' abundance and occupancy are shaped by species traits, using aquatic macroinvertebrates as an example. Based on the interrelations between species traits, life-history tactics have been defined for aquatic macroinvertebrates. Life-history tactics represent different solutions to a particular ecological problem, thus connecting species and their environment through species traits. Additionally, the relationship between a species' life-history tactic and its (realized) niche breadth was investigated.

A significant positive interspecific abundance-occupancy relationship is reported. Observed residuals from the abundance-occupancy relationship were significantly related to predictions based on differences in species traits. Furthermore, species with a broad niche were less abundant than species with a narrow niche, suggesting that the jack-of-all-trades may be master-of-none with respect to abundance. Relations between niche breadth and life-history tactics made sense intuitively. Species with a narrow niche had synchronised life cycles and low dispersal, being better adapted to predictable habitats, whereas species with a broad niche employed risk spreading and were strong dispersers, being better adapted to unpredictable habitats.

Differentiating between the various explanations underlying the positive interspecific abundance-occupancy relationship has been difficult. For instance, a similar (*i.e.* positive) relationship is predicted by each explanation and their assumptions are difficult to quantify (*e.g.* with respect to niche breadth or metapopulation structure). However, each explanation draws on several mechanisms that can be linked to differences in species traits. By translating mechanisms to relevant species traits and recognising how these are interrelated (for example in life-history tactics), explicit hypotheses can be constructed. Testing these hypotheses from a holistic approach based on species traits, may determine the relative importance of each explanation under different circumstances.

Introduction

A positive interspecific abundance-occupancy relationship across different species is one of the most robust patterns in macroecology (Brown 1984; Gaston & Lawton 1988; Brown *et al.* 1999). Identifying the underlying causal mechanisms is important as the abundance-occupancy relationship is intimately linked to species-area relationships and species-abundance distributions (Leitner & Rosenzweig 1997; McGill & Collins 2003; Heatherly *et al.* 2007). In addition, the nature of the explanation can have far reaching consequences for applied ecology, for example in predicting extinction risk and reserve selection (Lawton 1993; Brown *et al.* 1995; Gaston *et al.* 1999).

Intraspecifically, abundance and occupancy may be linked either directly through the dispersal of individuals or indirectly when environmental conditions are spatially autocorrelated (Brown *et al.* 1995). Explanations for interspecific abundance-occupancy relationships, reviewed by Gaston *et al.* (1997), also focus on the role of dispersal (metapopulation-based explanations) and environmental conditions (niche-based explanations). Metapopulation-based explanations suggest that locally abundant species (having a high carrying capacity) have a lower extinction rate and/or a higher colonization rate, thereby having better chances to become widespread (Nee *et al.* 1991). In addition,

widespread species have the best chances of filling up empty patches, thereby becoming locally abundant (Hanski & Gyllenberg 1993; Hubbell 1997). Niche-based explanations suggest that a species' niche breadth determines its abundance and occupancy. Both a species' environmental tolerances and resource requirements define the dimensions of a species' (multidimensional) niche (Hutchinson 1959). Species with a broad niche are able to use a wide range of resources and have broad environmental tolerances, which enable them to become both locally abundant and widespread (Brown 1984; Brown *et al.* 1995). It seems difficult to determine the validity of these explanations, because both explanations predict a positive interspecific abundance-occupancy relationship. Indeed, these and other explanations need not be mutually exclusive; each explanation may be valid under different circumstances (Gaston *et al.* 1997).

To disentangle the various explanations we propose to start from the mechanisms that lie at the base of a species' abundance and occupancy: species traits (Hengeveld & Walter 1999; McGill *et al.* 2006). Species traits that play a predominant role in shaping a species' abundance and occupancy are related to dispersal (Gutiérrez & Menendez 1997; Rundle *et al.* 2007) and reproduction (Blackburn *et al.* 1996; Holt *et al.* 1997). Species traits are not independent, but interrelated through functional combinations and trade-offs. For example, in aquatic macroinvertebrates, species with short-lived adults usually undertake few migration events and oviposit their eggs in a single or few large batches, while species with long-lived adults show directed migration and spread oviposition of single eggs or small batches over many locations. Additionally, hermaphroditic species whose effective breeding population is double that of bisexual species, usually lack active flight. Based on the interrelations between traits and their functional implications, life-history tactics for aquatic macroinvertebrates have been defined. Life-history tactics represent different solutions to particular ecological problems, thus connecting species and their environment through species traits (Chapter 3). Here we take aquatic macroinvertebrates in freshwater lentic habitats as an example to investigate the role of species traits (grouped in life-history tactics) in shaping interspecific abundance-occupancy relationships. In addition, the link between life-history tactics and (realized) niche breadth is explored.

Methods

Study area and sampling

The study was conducted in the nature reserve Korenburgerveen in the Netherlands (N: 51°59'; E 6°39'). In this heterogeneous wetland, 37 water bodies were sampled. Macroinvertebrates were collected using a standard 30 x 20 cm pond net with a mesh size of 0.5 mm. Sampling was aimed to obtain a species spectrum as complete as possible by sampling open water, vegetation and the littoral. Densities were calculated based on the area sampled. Samples were sorted in the laboratory. Tricladida, Hirudinea, Oligochaeta, Araneae, Crustacea, Megaloptera, Odonata, Hemiptera (adults and nymphs), Coleoptera (adults and larvae), Cylindrotomidae, Chaoboridae, Dixidae, Culicidae, Chironomidae and Trichoptera were identified to species level and used in the analysis. All water bodies were sampled twice (spring and autumn) and data from both seasons was combined. Preliminary analyses on either spring or autumn data generated strong and positive interspecific abundance-occupancy relationships. Combining the data from both seasons (in effect increasing the sample effort) strengthened the relationship, demonstrating that the relationship was not caused by a sampling artefact (Gaston *et al.* 1997).

Life-history tactics

Based on the interrelations between traits and their functional implications, 13 life-history tactics for aquatic macroinvertebrates have been defined (see Chapter 3). These life-history tactics differ in species traits that are considered relevant in shaping their abundance and occupancy. Based on these differences in species traits, we predicted the average abundance and distribution for each life-history tactic (Table 1).

Table 1 Overview of the life-history tactics and their most defining species traits in relation to distribution and abundance. For each life-history tactic, predicted average distribution and abundance are listed and a residual abundance is calculated, assuming a simple linear relationship (abundance = distribution).

Tactic	# Species	Active dispersal	Adult longevity	Synchronisation of juvenile development	Synchronisation of adult emergence	Type of oviposition	Clutch size	High voltinism	Hermaphroditism	Asexual reproduction	Distribution[a]	Abundance[b]	Predicted residual abundance
R3	3	none	months	low			small	x	x		1	4	3
R4	8	none		no	no				x	x	1	4	3
T2	7	none	months-years	no					x	x	1	3	2
R2	3	none	months	some					x		1	2	1
S4	13	none	months-years	yes			small		x		1	1	0
T1	49	low		low						(x)	2	3	1
S1	19	moderate	weeks		yes	clustered					2	3	1
S2	24	moderate		yes	yes	scattered					3	2	-1
S3	21	moderate	months-years	yes	yes	scattered					3	2	-1
R1	27	moderate	months-years			scattered	small				3	1	-2
D1	45	strong	months-years		some	scattered					4	2	-2
D2	4	strong			yes	clustered	large				4	4	0
D3	11	moderate		no	no	clustered		x		(x)	4	4	0

[a] classes of distribution: 1: very narrow; 2: narrow; 3: widespread; 4: very widespread
[b] classes of abundance: 1: very scarce; 2: scarce; 3: abundant; 4: very abundant

Species with no active dispersal (tactic R2, R3, R4, S4 & T2) are predicted to have a very narrow distribution. Species with a high rate of increase, either through multiple broods per season in combination with hermaphroditic reproduction (tactic R3), and asexual reproduction (tactic R4) are predicted to be very abundant. Species with mainly asexual reproduction but also investing in adult lifespan and tolerating harsh conditions (tactic T2) are predicted to be abundant. Species with a low rate of increase, resulting from a small clutch size and a single brood per season (tactic S4) are predicted to be very scarce. Species with low dispersal (tactic T1) or a moderate dispersal in combination with short-lived adults and a clustered oviposition (tactic S1) are predicted to be abundant and have a narrow distribution. Species having a moderate dispersal and a scattered oviposition (tactics S2, S3, & R1) are predicted to be widespread. Species with high dispersal (tactic D1, D2) or moderate dispersal in combination with a high voltinism (many dispersal events, tactic D3) are predicted to be very widespread. In addition, species with either a large clutch size (tactic D2) or a high voltinism (tactic D3) are predicted to be very abundant. With respect to abundance the remaining tactics (D1, R2, S2 and S3) are predicted to be scarce, unless they have a small clutch size (tactic R1), in which case they are predicted to be very scarce.

For each life-history tactic, a residual abundance is calculated, assuming a simple linear relationship (abundance = distribution). A species' abundance and occupancy results from the interplay between both its life-history tactic and the prevailing environmental conditions (Chapter 4). Therefore in practice, each tactic will be represented by species differing in the number of locations occupied and differing in abundance. However, we predict that observed differences in residual abundances (residuals from the abundance-occupancy relationship) between species from different tactics correspond to the predicted residual abundance (Table 1).

Niche breadth

To explore the link between life-history and (realized) niche breadth, we calculated the niche breadth for each species observed in our study. A species' niche breadth should be based on the relevant niche axes. Although Hutchinson's multidimensional niche is assumed to be constant on an ecological time scale, prevailing biotic as well as abiotic conditions give rise to local variation in a species' realized niche. Therefore, we adopt a somewhat narrower but more operational measure of a species' niche and express niche breadth as the specificity of a species for a certain water type. Sampled water bodies were classified into three main water types and eight subtypes, based on differences in environmental conditions (nutrient concentrations, acidity, alkalinity, soil type, dimensions, degree of shading and vegetation composition). Average values for different physical and chemical properties of the subtypes are listed in table 2. These water types reflect relevant differences in environmental conditions for aquatic macroinvertebrates (Chapter 2 and 4), thereby providing a meaningful approximation of a species' realized niche.

Classifying species by niche breadth should be independent of a species' abundance and occupancy to prevent that abundant and widespread species will have a wider niche simply because they have a higher chance to be sampled from more locations. To prevent this, we included both the range in water types (measure of fidelity, see below) under which a species is present, and its numerical response across this range (measure of aggregation, see below). To classify species independent of their abundance and occupancy, range and response were expressed as relative numbers (*i.e.* related to the total number of sampled water bodies and the total number of individuals). For each species j and water type or water subtype i we calculated:

1. a measure of fidelity (FI), taking on values between 0 and 1, and a value of 1 indicating that a species occurred in a single water(sub)type only:

$$FI = \underset{i}{MAX} \left\{ \frac{\text{\# water bodies of water(sub)type i occupied by species j}}{MIN \begin{cases} \text{total \# water bodies occupied by species j} \\ or \\ \text{total \# water bodies of habitat i} \end{cases}} \right\} \qquad \text{(eq. 1)}$$

2. a measure of aggregation (SI), with high values indicating high aggregation. This is the reciprocal of Schoener's selectivity index (Schoener, 1974):

$$SI = \sum_{i} \left\{ \frac{(\text{\# individuals of species j in water(sub)type i / total \# individuals of species j})^2}{(\text{total area sampled in water(sub)type i / total area sampled})^2} \right\} \qquad \text{(eq. 2)}$$

Table 2 Subdivision of the 37 sampled water bodies in three main water types and eight water subtypes. Differences in physical and chemical conditions between the different water types are shown as averages ± standard error.

Main type	Water type	# water bodies	pH	Alkalinity (meq.l⁻¹)	o-PO$_4^{3-}$ (μmol.l⁻¹)	NO$_3^-$ (μmol.l⁻¹)	NH$_4^+$ (μmol.l⁻¹)	Size (m²)	Depth (cm)	Shading (%)	Temporary[1]
Bog pools	large bog pools	6	3.7±0	0±0	1.4±0.4	4.3±0.6	16.1±6	34±15	0.5±0.2	27±9	0±0
	small bog pools	5	3.8±0.1	0±0	1±0.3	5±0.6	45.6±15.7	19±10	0.5±0.1	32±7	0.1±0.1
	small, shaded bog puddles	4	3.8±0.1	0±0	1.9±0.7	5.1±0.9	55±17.3	5±3	0.5±0.3	51±25	0.3±0.3
Water bodies in wet forests	water bodies in *Salix-Betula* forests	3	5.1±0.6	0.31±0.25	2.2±1.2	3±0.5	21.1±4.8	22±4	0.4±0	51±27	0.4±0.1
	water bodies in *Salix-Alnus* forests	7	6.2±0.3	1.63±0.43	1.4±0.5	41.4±26.6	47.5±21.4	25±7	0.3±0.1	56±17	0.4±0.2
Mesotrophic waters	shallow mesotrophic puddles	3	5.3±0.5	0.25±0.1	0.6±0.2	4±0.1	12.1±3.5	20±4	0.4±0.1	30±13	0.3±0.2
	large mesotrophic pools	5	5.7±0.2	0.36±0.16	0.5±0.2	4.6±0.8	9.7±2.2	408±236	1.1±0.2	13±5	0±0
	strongly buffered mesotrophic pools	4	6.5±0.2	1.13±0.24	1.3±0.7	1.8±0.2	7.3±1	128±55	0.8±0.1	25±4	0.1±0.1

[1] Indicating the proneness to dessication of a water body, ranging from 0 (permanent) to 1 (temporary)

Next, for each species, these two measures were equally weighted by multiplying them (FI *SI), generating a combined index (where high values indicate a high specificity for a certain water type). This index was calculated separately for the three main water types and the eight water subtypes. No reliable measure of niche breadth could be calculated for species captured in only one water body and these were therefore excluded from analyses involving niche breadth. Percentiles (50% and 75%) were calculated across all species for the combined indices for water type and water subtype separately. Species were classified as having a broad niche if both indices fell below the 50-percentile. Species were classified as having an intermediate niche breadth if their index for water type was above the 50-percentile and their index for subtypes was below the 75-percentile. The remaining species were classified as having a narrow niche.

Data analysis
For the remainder of this article, a species' frequency of occurrence indicates its occupancy, while a species' average density (# individuals per m^2, averaged across all sites where it is present) indicates its abundance. Abundance was log-transformed (base 10) to improve normality. To test whether there was a relationship between the abundance and occupancy of species, a linear regression was used taking species as replicates and abundance as the dependent factor. Residuals from the abundance-occupancy relationship are referred to as residual abundances. To test whether there was a relationship between the observed and predicted residual abundance, a linear regression was used taking species as replicates and observed residual abundance as the dependent factor. A General Linear
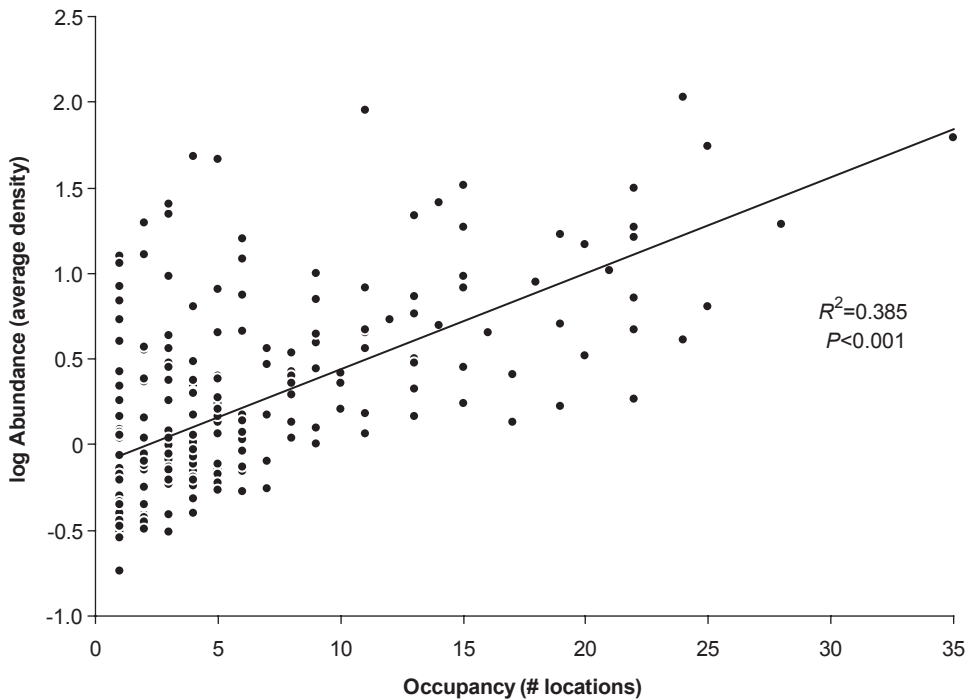

Figure 1 Interspecific relationship between log abundance (number of individuals per m^2 averaged for all occupied water bodies) and occupancy (number of occupied water bodies). Each data point represents a different species.
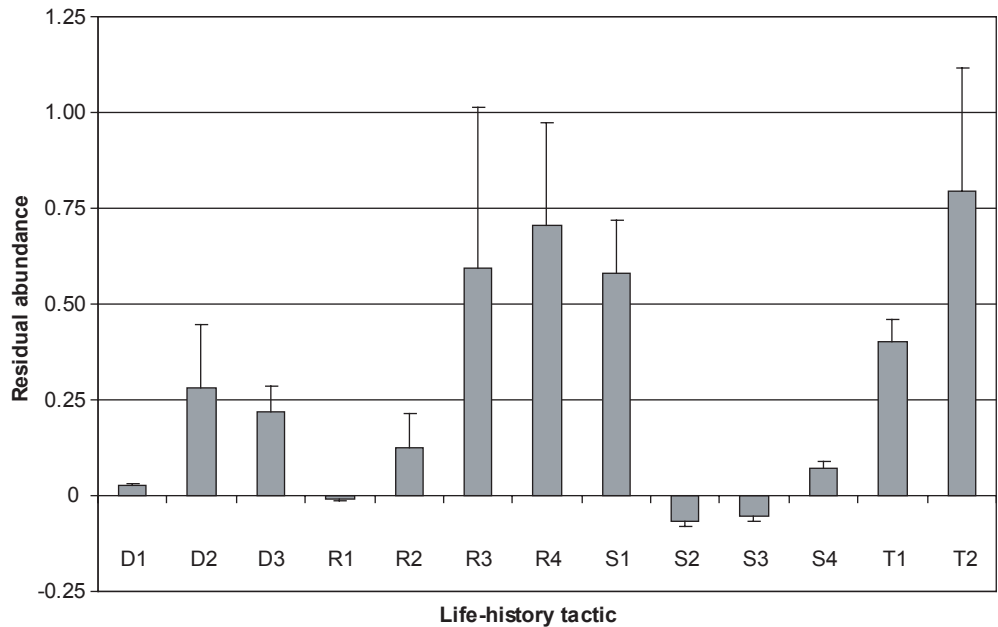
Figure 2 Residual abundance (averages ± standard error) of species in each life-history tactic. For each life-history tactic, the abbreviations, the number of species and the defining species traits are listed in Table 1.

Model (GLM) was used to test for significant differences in abundance and occupancy between species differing in niche breadth. For both linear regressions and GLM analyses, residual plots were checked for normality. Homogeneity of variance was tested using a Levene's test. All statistical analyses were performed using SPSS version 15.0.

Results

A significant interspecific relationship between the abundance and occupancy of the various aquatic macroinvertebrate species was demonstrated (Fig. 1). Species occupying many water bodies were frequently also more abundant in these water bodies, although there was considerable scatter. Residual abundances (residuals from the abundance-occupancy relationship) differed between species assigned to different life-history tactics (Fig. 2; Kruskal Wallis test: $P<0.001$). Species without active dispersal and a high intrinsic rate of increase (tactic R3, R4 & T2) showed high residual abundance, being more abundant than expected based on their occupancy (or vice versa, having a lower occupancy than expected based on their abundance). In contrast, species with widely scattered oviposition and moderate or strong active dispersal (tactic R1, S2, S3 & D1) showed low residual abundance, being less abundant than expected based on their occupancy. These results corresponded to predicted residual abundance (Table 1; Fig. 3). A linear regression between predicted and observed residual abundance was highly significant ($R^2=0.144$; Beta 0.380; $P<0.001$).

Abundance, but not occupancy differed between species grouped by niche breadth (Fig. 4; GLM analysis: $P<0.01$). Species with a broad niche were less abundant than species with a narrow niche. Life-history tactics were not evenly distributed across species
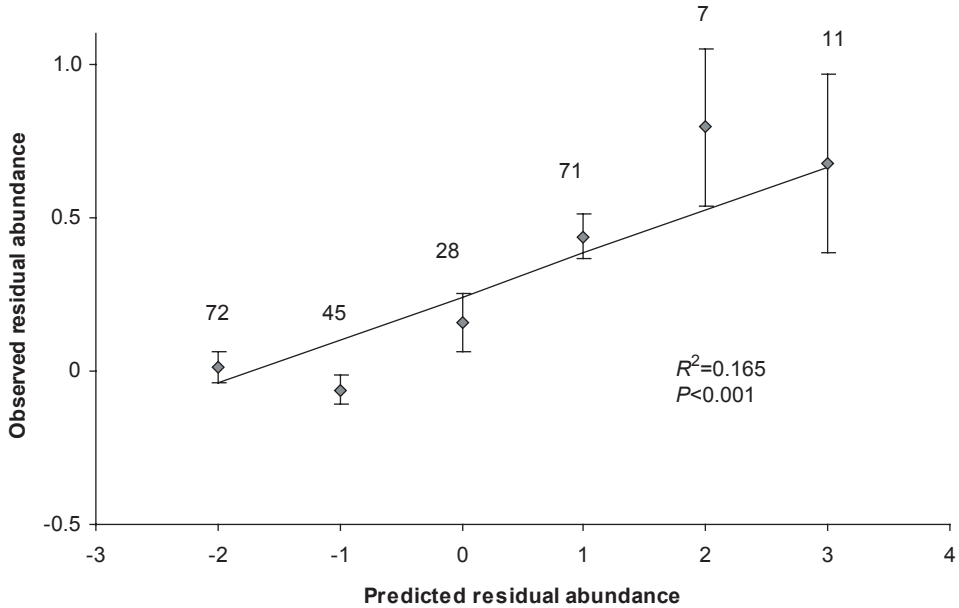
Figure 3 Relationship between observed residual abundance (averages ± standard error) and predicted residual abundance (see Table 1). Averages are calculated over all species (numbers indicate the number of species) with the same predicted residual abundance.

groups based on niche breadth (Fig. 5; χ^2 test: $P<0.001$). Many species with a synchronized life cycle (tactics S1, S2, S3 & S4) or lacking active dispersal (tactics T2 & R4) had either a narrow niche or an intermediate niche breadth. In contrast, many species with long-lived adults, spreading reproductive effort in time and space (tactics D1, R1, R2 & R3) had a broad niche.

Figure 4 Occupancy (left) and abundance (right) for species grouped by niche breadth (n equals the number of species in each group). Averages + standard error are shown. Significant differences ($P<0.05$) are indicated by different letters, based on Games-Howel post-hoc tests.

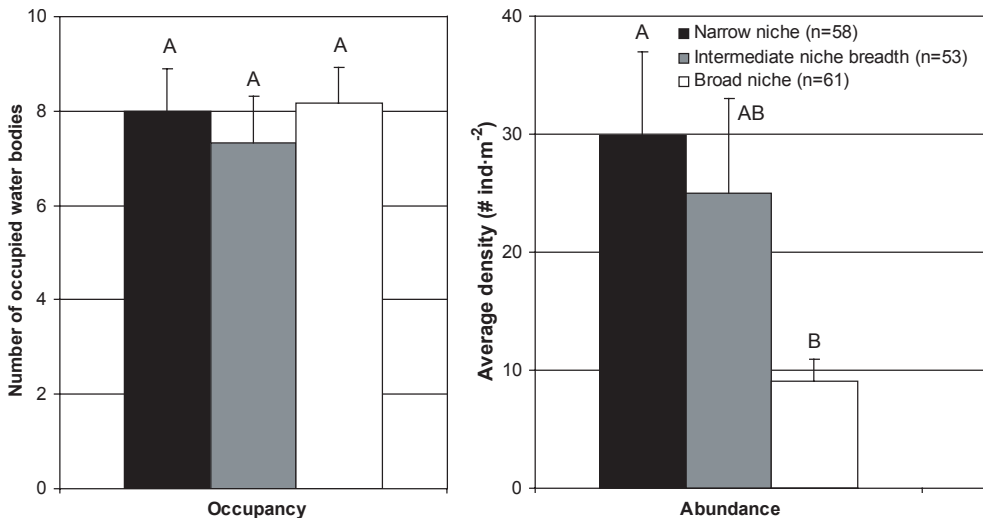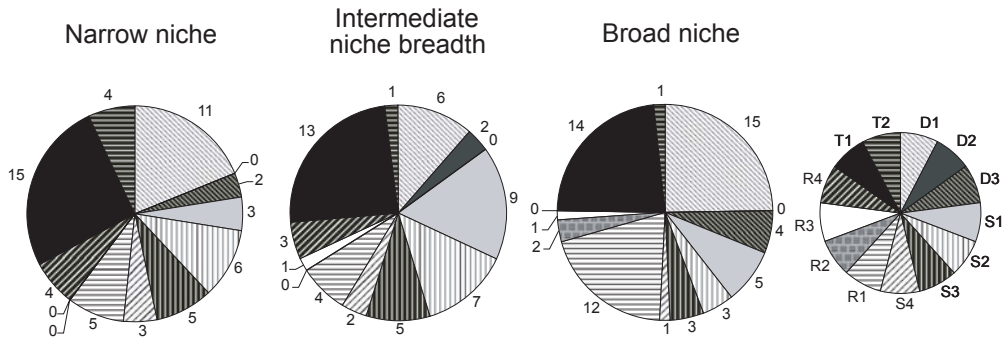**Figure 5** Distribution of life-history tactics across species groups based on niche breadth. Numbers indicate the number of species. For each life-history tactic, the abbreviations and defining species traits are listed in Table 1.

Discussion

A positive interspecific abundance-occupancy relationship for aquatic macroinvertebrates is reported in this study (Fig. 1). Although the majority of studies focus on ecologically similar groups such as birds, butterflies, dragonflies, fish (Blackburn *et al.* 1997; Cowley *et al.* 2001a; Rundle *et al.* 2007; Tales *et al.* 2004; but see Gaston & Lawton 1988), here we show that the relationship also exists across an assemblage of species from various systematic groups such as aquatic macroinvertebrates. Furthermore, we found a good agreement between the observed and the predicted residual abundances (residuals from the abundance-occupancy relationship) for the different life-history tactics based on differences in species traits (Fig. 3). This demonstrates that species traits combined in life-history tactics generate theoretical predictions which are upheld, despite variation encountered in practice, arising for example due to the underlying spatial distribution of environmental conditions.

Current explanations underlying the positive interspecific abundance-occupancy relationship lack clear definitions and make assumptions that are difficult to quantify (*e.g.* with respect to niche breadth or metapopulation structure). In this study we have analysed how species traits, combined in life-history tactics, shape a species' abundance and occupancy. As species traits are basic, well-defined properties of a species, such an approach is promising. Given the fact that the proposed explanations have the same prediction (a positive relationship; Hartley 1998) and may be acting in concert (Heino 2005), residuals may provide more information on the relative importance of the mechanisms underlying the interspecific abundance-occupancy relationship (Cowley *et al.* 2001b). By focussing on the residual abundances (residuals from the abundance-occupancy relationship), we found a good agreement between the observed and the predicted residual abundances for the different life-history tactics. Previous studies that have attempted to relate residuals to interspecific differences (*e.g.* in habitat use, feeding guild, mobility or body size) have been largely unsuccessful (Blackburn *et al.* 1997; Quin *et al.* 1997). Holt & Gaston (2003) even "doubt the generality of such an approach and its future role in understanding the determinants of abundance-occupancy relationships".

This contrasts with our findings of a strong significant relation between predicted and observed residual abundance, for which we offer four reasons.

First, in our study we included many different species with fundamentally different life-histories, providing the necessary contrasts in life-history. Second, all species used a similar habitat (water bodies), notwithstanding differences in life-histories. Third, we based our predictions only on species traits that are independent from prevailing environmental conditions, rather than including emergent features such as habitat use or niche breadth. The fourth and last reason stems from how we dealt with interrelations between species traits. Species traits are strongly interrelated through functional combinations and trade-offs and their adaptive value depends on the entire species' biology (Gould & Lewontin 1979; Chapter 3). Therefore, controlling for phylogenetic relatedness, pulls traits out of their phylogenetic context and consequently the functional implication of trait combinations is lost. For example, expectations for mobile and *semelparous* species (*e.g.* tactic S1) differ radically from mobile and *iteroparous* species (*e.g.* tactic R1). Moreover, alternative trait combinations that are functional equivalent are not detected. By grouping species in life-history tactics these issues are dealt with.

A species' abundance was also related to its niche breadth. Like many other studies (*e.g.* Brown 1984; Thompson *et al.* 1988; Cowley *et al.* 2001a; Chase & Leibold 2003), this indicates that elements of niche are involved in determining species abundances. The present study demonstrates that species with a narrow niche showed higher abundances than species with a broad niche (Fig. 4). This confirms the views held for freshwater habitats (Brönmark & Hansson 2005), but contrasts with Brown's (1984) hypothesis, which stated that species with a broad niche are both locally abundant and widespread. Although many studies report a positive relationship between niche breadth and *occupancy* (Gaston & Spicer 2001; Heino 2005; Cowley *et al.* 2001b), studies on the relationship between niche breadth and *abundance* frequently report no or even a negative relationship (Thompson *et al.* 1998; Päivinen *et al.* 2005; Gaston *et al.* 1997). In French riverine fish, body size was negatively correlated with abundance but positively with occupancy (Tales *et al.* 2004). Together with our results these studies indicate that the assumption that both a species' abundance and occupancy are simultaneously and equally affected by a species' niche breadth is invalid. It appears that the jack-of-all-trades (*i.e.* species with a broad niche) may be master-of-all with respect to occupancy, but master-of-none with respect to abundance.

The difficulty with niche-based explanations is that they are difficult to refute; one can always maintain that the relevant niche axis has not been measured (Gaston *et al.* 1997). This problem can be circumvented by relating niche breadth to species traits, which are basic, well-defined properties of a species which can be measured relatively straight forward. Relating niche breadth to species traits, combined in life-history tactics, yielded results that made sense intuitively (Fig. 5). Species with a narrow niche were better adapted to stable, predictable habitats, with many species having synchronised life cycles and low dispersal. In contrast, species with a broad niche were better adapted to unstable habitats, having a high dispersal and employing risk spreading. McAbendroth *et al.* (2005) report a similar co-occurrence of traits on dispersal and ecological tolerance for aquatic macroinvertebrates in heathland ponds. They found that nested taxa had narrow tolerances and limited powers of dispersal, while idiosyncratic taxa (showing no nested structure) possessed a broad ecological tolerance and good dispersal capacities. These findings show that niche breadth can be linked to species traits, combined in life-history

tactics. Because species traits are independent from prevailing environmental conditions, they offer a more parsimonious explanation for interspecific differences in abundance and occupancy than niche breadth.

Under the traditional views it was difficult to explain the existence of habitat specialisation, as specialists were supposedly restricted and scarce, and therefore prone to extinction (Lawton 1993). To compensate extinction, high speciation rates were invoked (Brown 1984). With the alternative presented here, species with a broad niche can persist by spreading risks of reproductive failure, being present in a variety of different habitat types. Conversely, species with a narrow niche can persist through numerical larger local populations, suggesting that specialisation is an evolutionary stable strategy. Another consequence is that for species with a narrow niche a larger part of the population will be affected by local perturbation (*e.g.* effects of habitat destruction and degradation).

In conclusion, testable predictions can be constructed regarding the effect of species trait combinations on a species' abundance and occupancy. Although many different explanations exist for interspecific abundance-occupancy relationships, each explanation draws on several mechanisms that can be linked to differences in species traits. We have shown that niche breadth can be related to differences in species traits related to dispersal, reproduction and synchronisation. Thus a species' relative abundance and occupancy can be linked to the combination of traits it possesses. A similar approach may be followed to test the effect of factors such as biotic interaction (Holt *et al.* 2002), spatial aggregation (Hartley 1998), or even differences in ecosystem characteristics (Blackburn *et al.* 2006) on the interspecific abundance-occupancy relationship, by selecting relevant species traits and recognising how these are interrelated. Testing such predictions from an integrative approach based on species traits may bring about a synthesis of the various explanations and determine their relative importance under different circumstances.

Acknowledgements

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One of the sampled water bodies in Salix-Betula forests with flowering water violet (Hottonia palustris) on 03 May 2004. At this location, the chemical composition of pore water and surface water indicated an increase of groundwater influence (type 2+). Photo: Wilco Verberk.

Chapter 6

Restoration measures induce homogenisation in a bog landscape - response of aquatic macro-invertebrates to rewetting measures

Verberk WCEP, RSEW Leuven, GA van Duinen & H Esselink

Summary

Restoration management frequently focuses on recreating the proper physico-chemical conditions for a target vegetation, assuming that recovery of plant and animal species will follow automatically. Such a focus may be too narrow, neglecting the importance of environmental heterogeneity for animal species.

This study investigates the importance of environmental heterogeneity in a restoration context. It reports the response of aquatic macroinvertebrates to restoration measures, which were taken to mitigate desiccation in a bog landscape. To functionally interpret the response of aquatic macroinvertebrates, species were grouped in life-history tactics. Life-history tactics are based on the relations between species traits and their functional implications. Life-history tactics represent different solutions to particular ecological problems, thus connecting species and their environment through species traits.

Effects of restoration measures on environmental conditions could be consistently related to changes in composition of life-history tactics (species abundances pooled per life-history tactic). Retention of rainwater increased water tables and decreased the influence of groundwater. Species with a high tolerance and species that employed risk spreading increased, indicating environmental conditions had become harsher and less predictable. Reduced drainage locally increased groundwater, enhancing predictability of environmental conditions, which promoted species with a synchronised life cycle. Large-scale retention of rainwater decreased environmental heterogeneity. Cumulative numbers of species declined in the rewetted parts and life-history tactic composition became more similar. These results indicate that rewetting acted as a species filter, promoting the expansion of a few life-history tactics at all water bodies, while constraining the other tactics.

Our results show that increasing the supply of groundwater is a promising restoration strategy for aquatic invertebrates in degraded bog remnants. Here, cumulative numbers of species did not decline. Moreover, bogs have primarily developed through succession from minerotrophic to acidic peat lands, and it was recently shown that also secondary succession is stimulated by minerotrophic groundwater in the base of the peat substratum. Increased supply of minerotrophic groundwater gradually gives rise to stable, minerotrophic transitions, which are important hotspots for biodiversity in pristine raised bog landscapes. Restoring such natural processes driving heterogeneity may increase the effectivity of restoration plans for animals by restoring both ecosystem functioning and structure.

Introduction

Restoration measures aim to counter the negative effects of degradation. Ecosystem restoration ranges from repeated intervention to speed up the recovery process to merely removing barriers that impede recovery, giving room to natural processes. In many cases, restoration focuses on recreating the proper physico-chemical conditions for a target vegetation (Young 2000), assuming that the recovery of plant and especially animal species will occur automatically sooner or later (Palmer *et al*. 1997; Dobson *et al*. 1997). Such a focus may be too narrow as degradation impacts on two interlinked ecosystem components (Bradshaw 1996): ecosystem functioning (*e.g.* nutrient cycling, productivity) and ecosystem structure (including the various species and the spatial arrangement of their habitats). Thus, following the impact of degradation not only processes (ecosystem

Figure 1 Pallisade timber dam lining compartment 2 in early spring 2002. Photo: Wilco Verberk

functioning), but also the diversity of habitats and their spatial arrangement (ecosystem structure) need to be restored.

Environmental heterogeneity, consisting of the diversity of habitats and their arrangement on a wide variety of scales, affects species persistence (*e.g.* Brown 2003), shapes species interactions (*e.g.* Amarasekare 2003) and is an important driver of plant and animal diversity (Dennis *et al.* 1998; Huston 1999; Heino 2000). Animal species in particular use and require environmental heterogeneity, as they (need to) move between different patches, each providing different functions (*e.g.* reproduction, hibernation and foraging) during their life cycle (Dunning *et al.* 1992; Chapter 2).

The importance of environmental heterogeneity in a restoration context remains largely untested (Palmer *et al.* 1997). Here we report the response of aquatic macroinvertebrates to restoration measures, which were taken to mitigate desiccation in a bog landscape. An important objective of these restoration measures is to promote *Sphagnum* growth, which is regarded as an ecosystem engineer that creates its own optimal environment (permanently wet, acid and nutrient poor conditions) (van Breemen 1995; Rochefort 2000). To this end drainage ditches were filled and dams were constructed to retain rainwater (Fig. 1) in different hydrological compartments (Fig. 2). This type of measures is common practice in the restoration of degraded bogs throughout western Europe (Wheeler & Shaw 1995). These measures can be characterised as a single intervention aimed at removing an important barrier (desiccation) to ecosystem recovery. Because the measures have a similar impact over a large area, environmental heterogeneity may decrease.

In this study, aquatic macroinvertebrates were sampled both before and after measures were taken. To understand how effects of restoration measures are related to changes in species composition, knowledge of the causal mechanisms underlying documented changes is required. Life-history tactics may provide such understanding as they are based on a functional interpretation of a species' adaptations (Chapter 3). Life-history tactics can be seen as a species' integrated response to the environment. Studying changes in life-history tactic composition in species samples provides information on how the environment is experienced by the species present (Chapter 4). Specifically the following questions are addressed:
1) What are the changes in life-history tactic composition and how are they related to the effects of restoration measures?
2) Have water bodies within the same compartment become more similar with respect to life-history tactic composition, indicating a decline of environmental heterogeneity?
3) What are the changes in species diversity and species turnover and how are they related to the effects of restoration measures?

Methods

Data collection
The water bodies sampled are located in the heterogeneous bog remnant Korenburgerveen. In total 45 water bodies were sampled, distributed throughout the research area (Fig. 2). Based on differences in environmental conditions (nutrient concentrations, acidity, alkalinity, soil type, dimensions, degree of shading and vegetation composition), the water bodies were classified into three water types: mesotrophic waters, water bodies in wet forests and bog pools (Table 1). Further details on the study area, environmental conditions and typology are given in Chapter 2.

Water bodies were sampled in 2000-2002 before measures were taken. All water bodies were resampled in 2004. Samples were collected using a standard pond net of 30 x 20 cm with a mesh size of 0.5 mm. Sampling was restricted to spring (April-May) and autumn (October-November). Samples were washed and sorted in the laboratory. Tricladida, Hirudinea, Oligochaeta, Araneae, Crustacea, Odonata, Hemiptera, Coleoptera, Cylindrotomidae, Chaoboridae, Dixidae, Culicidae, Chironomidae and Trichoptera were identified to the lowest taxonomic level possible, which was in most cases species level.

Table 1 Overview of the number of sampled water bodies per water type, type of change (see table 2) and hydrological compartment. Hydrological compartments and the location of the sampled water bodies are shown in figure 2.

| Water type | | Type of change | | | | | Hydrological compartment | | | | | | |
Description	# sites	1	2-	2+	3-	3+	1	2	3	4	5	6	7
Mesotrophic water bodies	14	9	2	1	2		1		1	8	1	1	2
Water bodies in wet forests	13	4	7	2			2		2		4	4	1
Bog pools	18	7	2		5	4	2	10	5				1

Changes in environmental conditions
For each sampled water body, we assessed if changes had occurred in either the vegetation composition or physical and chemical properties of the water body. Three types of changes were distinguished (Table 1 and 2). In 20 of the 45 water bodies no or only minor
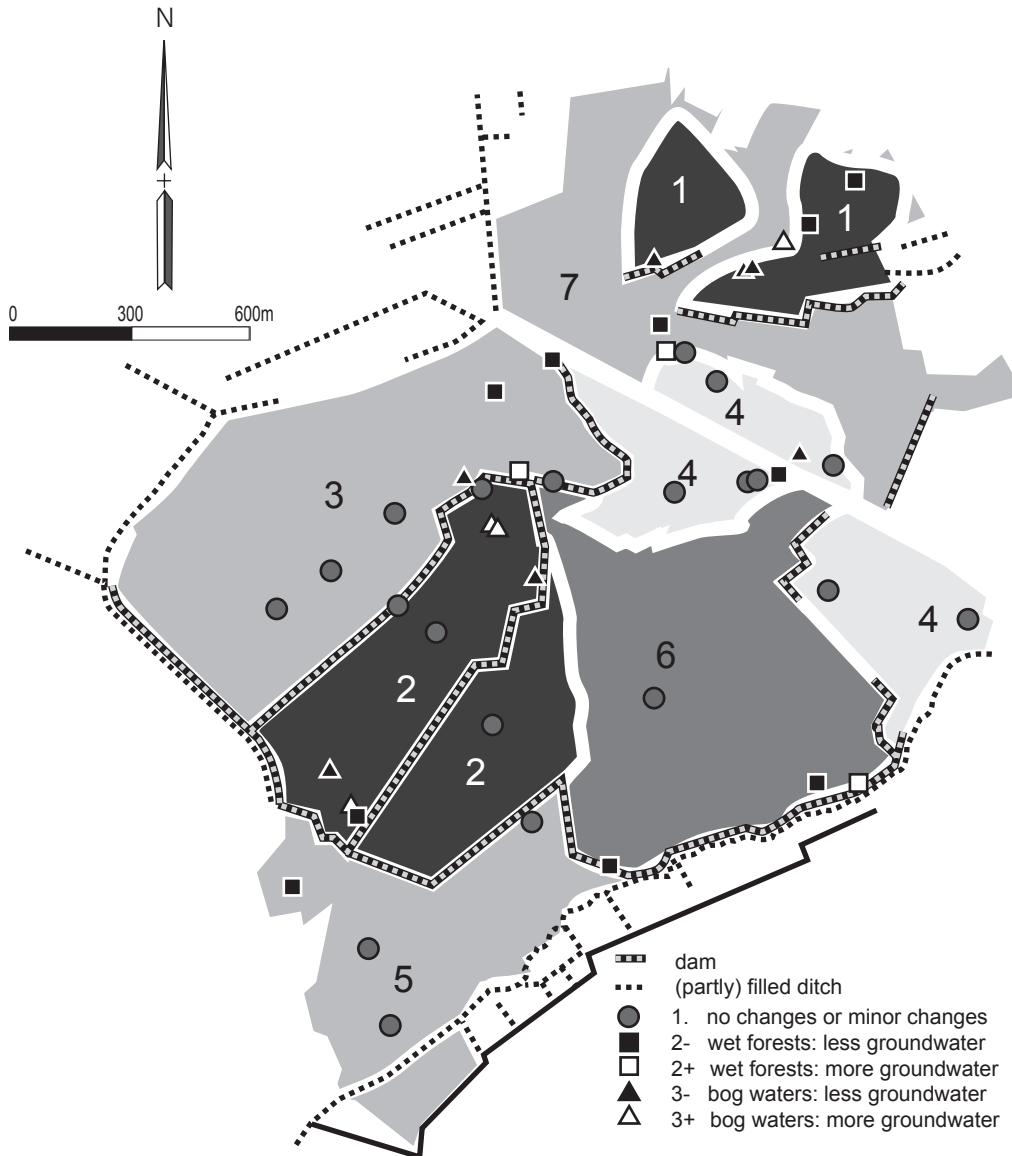
Figure 2 Subdivision of the research area into seven different hydrological compartments (indicated by numbers) and the location of the sampled water bodies. Different symbols indicate different types of change (see table 2). Restoration measures (construction of dams and filling of ditches) are also indicated.

changes in environmental conditions had occurred (type 1). These water bodies were subdivided according to their original water type. In the remaining 25 water bodies environmental conditions changed with respect to groundwater influence (changes in alkalinity and levels of Ca^{2+}), nutrient availability (changes in ortho-phosphate and total Nitrogen) and vegetation cover. Additionally, higher water tables and changes in the stagnation of water were observed.

Table 2 Changes in selected physico-chemical variables and vegetation cover of *Eriophorum angustifolium* and *Glyceria fluitans* following restoration measures for each type of change. Averages values and standard error are shown.

Type of change	Before/After measures	Groundwater influence			Nutrient availability		Physical variables		Vegetation cover[1]	
		pH	Alkalinity (meq.l⁻¹)	Ca^{2+} (µmol.l⁻¹)	$o\text{-}PO_4^{3-}$ (µmol.l⁻¹)	Total N (µmol.l⁻¹)	Shade (%)	Depth (m)	*E. angusti-folium*	*G. fluitans*
1 no or minor changes (n=20)	B	5.1 (0.3)	0.54 (±0.19)	317 (±98)	1.1 (±0.2)	26 (±7)	30 (±5)	0.6 (±0.1)	1.6 (±0.3)	0.0 (±0.0)
	A	4.9 (±0.3)	0.86 (±0.34)	397 (±124)	0.8 (±0.3)	24 (±4)	25 (±10)	0.9 (±0.1)	3.6 (±0.8)	0.3 (±0.2)
2- wet forests (n=11) less groundwater	B	5.7 (±0.3)	1.08 (±0.33)	525 (±171)	1.4 (±0.4)	47 (±29)	70 (±10)	0.4 (±0.1)	0.2 (±0.2)	0.6 (±0.3)
	A	5.5 (±0.2)	1.12 (±0.49)	398 (±85)	4.7 (±2.4)	64 (±32)	50 (±10)	0.6 (±0.1)	1.2 (±0.8)	3.0 (±1.1)
2+ wet forests (n=3) more groundwater	B	5.9 (±0.6)	0.98 (±0.70)	476 (±250)	2.3 (±0.8)	36 (±13)	80 (±10)	0.4 (±0.1)	0.0 (±0.0)	1.0 (±0.7)
	A	5.7 (±0.5)	4.55 (±5.21)	708 (±567)	0.9 (±0.3)	20 (±10)	55 (±20)	0.7 (±0.1)	0.0 (±0.0)	4.3 (±2.9)
3- bog pools (n=7) less groundwater	B	4.1 (±0.3)	0.06 (±0.04)	127 (±36)	0.9 (±0.2)	33 (±9)	55 (±15)	0.6 (±0.2)	1.0 (±0.3)	0.0 (±0.0)
	A	3.8 (±0.1)	0.00 (±0.00)	136 (±20)	0.8 (±0.4)	14 (±2)	25 (±15)	0.9 (±0.2)	5.0 (±0.6)	0.0 (±0.0)
3+ bog pools (n=4) more groundwater	B	3.7 (±0.1)	0.00 (±0.00)	63 (±14)	1.2 (±0.4)	53 (±17)	35 (±25)	0.3 (±0.1)	3.5 (±1.8)	0.0 (±0.0)
	A	4.0 (±0.2)	0.10 (±0.09)	132 (±21)	1.0 (±0.5)	24 (±3)	25 (±15)	0.6 (±0.4)	5.8 (±1.3)	0.0 (±0.0)

The multitude of the environmental changes and combinations thereof can be simplified because many changes co-occur. For example, water stagnation lowers the redox potential, stimulating the reduction of sulphate to sulphide, which can bind to iron-phosphate complexes. This process results in the formation of pyrite (FeS) and the mobilisation of phosphate and is called internal eutrophication (Lucassen 2004; Smolders *et al.* 2006). In addition higher water tables can cause trees to die, decreasing the degree of shading. Concomitantly, the aquatic vegetation responds to changes in shading and phosphate. Changes in environmental conditions also depended to some extent on the initial situation, which differs between water types. Therefore, for the 25 changed water bodies a distinction was made between shaded water bodies with higher nutrient concentrations and low acidity (type 2, most changed water bodies in wet forests) and more acidic water bodies with low nutrient concentrations (type 3, most changed bog pools).

Water bodies in type 2 were further subdivided in those where higher water tables caused a decrease of groundwater influence (type 2-) and those where groundwater influence increased (type 2+). Decreased groundwater resulted in a combination of several of the following effects: stagnation of water, internal eutrophication, less shading or an increase of vegetation (mainly *Glyceria fluitans*) (Table 2). These effects were absent or reversed in water bodies with increased groundwater. Water bodies in type 3 were also subdivided in those were higher water tables caused a decrease of groundwater influence (type 3-) and those where groundwater influence increased (type 3+). Here decreased groundwater and increased water tables primarily decreased the degree of shading and increased cover of vegetation (mainly *Eriophorum angustifolium*) (Table 2).

Life-history tactics

To understand how changes in environmental conditions affect aquatic macroinvertebrates species composition, we used a functional classification where species are grouped based on species traits. Using species traits provides insight in the causal mechanisms underlying documented changes (McGill *et al.* 2006). The large variety in these traits presents a problem when trying to group species based on species traits. We solved this problem by investigating how traits are interlinked through trade-offs and spin-offs, thereby reducing the number of trait combinations. In addition, from these interrelations we interpreted the function of trait combinations (*e.g.* reduce egg mortality, speed up development, spread risks). This allowed us to distinguish between species groups that solve environmental problems in a similar way, thus connecting species and their environment through species traits. These groups are referred to as life-history tactics (described in more detail in Chapter 3 and 4). In total 13 life-history tactics were distinguished, differing in dispersal, growth rate and duration of growth period, degree of synchronisation of juvenile growth or adult emergence or both, and reproduction rate (number of eggs and voltinism) (Table 3; Appendix 1).

Data analysis

For all analyses, data from spring and autumn and data on different life stages (larvae, nymphs, pupae and adults) of the same species were pooled. For each water body sampled, the numerical contribution of each species was expressed as a percentage of the total number of individuals. Percentual contributions of taxa belonging to the same tactic were pooled, resulting in a tactic composition per sampled water body. Next, we

Table 3 Overview of the different life history tactics and their most defining species traits. Less defining species traits and species traits varying within a tactic are left blank.

Tactics		Juvenile development	Period of juvenile development	Adult life span	Dispersal	Per capita investment	Synchronisation of juvenile development	Synchronisation of adult emergence	Voltinism	Tolerance to adverse abiotic conditions	Genetic recombination
Dispersal	D1	rapid		months-years	strong active dispersal			some			
	D2		long		strong active dispersal	low, large clutch size		yes	semi-univoltine		
	D3	rapid[1]	short				no	no	bi-multivoltine		low
Synchronisation	S1		long	weeks				yes			
	S2	rapid					yes[4]	yes[4]	univoltine		
	S3	rapid		months-years			yes				
	S4	rapid		months-years	no active dispersal	high	yes		univoltine		
Developmental trade-off	T1	slow			low active dispersal		low			high	
	T2	slow	long	months-years	no active dispersal		no			high	low
Reproduction	R1	rapid		months-years		high[2]					
	R2	slow		months	no active dispersal	moderate	some				
	R3	rapid		months	no active dispersal	high[2,3]	low		bi-multivoltine		
	R4	rapid[1]	short		no active dispersal		no	no			low

[1] Early age at first reproduction, [2] Protracted oviposition period, [3] Parental care, [4] Diapausing, resistant stages

compared the tactic composition of groups of sampled water bodies before and after the rewetting measures. Changes in life-history tactic composition were tested using either a one way ANOVA (normally distributed data from more than ten water bodies) or a Wilcoxon signed rank tests (data from less than ten water bodies).

To examine the extent of the shift in tactic composition and species composition we calculated for each sampled water body the similarity index between the situation before and after the rewetting measures. For the tactic composition we used the Bray-Curtis similarity index taking abundances into account (Bray & Curtis 1957) and for the species turnover we used the Sørensen similarity index (Sørensen 1948). Furthermore, we calculated the number of species gained and lost for each sampled water body. Next, we averaged these numbers across groups of water bodies with a similar type of change. In addition, the total (cumulative) number of species lost and gained was calculated for groups of water bodies with a similar type of change.

To test whether there was a decrease in species turnover or beta diversity for water bodies located within the same compartment, species accumulation curves were generated using BioDiversity Professional Beta 1 (McAleece 1997). Curves were based on averages of 500 random permutations of the sample sequence. In addition, we tested whether

sampled water bodies located within the same compartment had become more similar in life-history tactic composition after the rewetting measures, by calculating the similarity in tactic composition for all pairs of sampled water bodies (990 possible combinations for 45 water bodies), both before and after the rewetting measures. Next, we averaged the similarity for all combinations where the pair of sampled water bodies was located within the same compartment (137 combinations) and for all combinations where the pair of sampled water bodies was located in different compartments (853 combinations). Student t-tests were used to test for significant difference between sample periods (before or after the rewetting measures). Significance levels were corrected for by recalculating them based on 44 degrees of freedom (number of sampled water bodies -1).

Results

The composition of life-history tactics (species abundances pooled per life-history tactic) during the first sample period, differed from the composition of life-history tactics during the second sample period (Table 4). These changes were related to the effect of restoration measures as expressed in type of change (Table 4; Fig. 3).
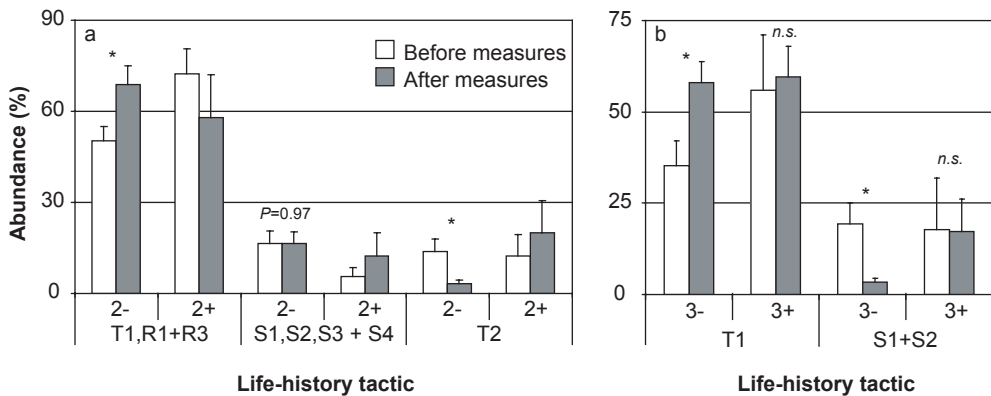
Figure 3 Dominant changes in life-history tactics for changed water bodies in wet forests (a) and bog pools (b). Asterisks denote significant differences (P<0.05). Changes in other tactics are listed in table 4.

Changed water bodies in wet forests, where groundwater influence decreased (type 2-) showed an increase of species that have a fast development and multiple successive reproduction attempts (tactic R1 & R3) and species that have a high tolerance for unfavourable conditions (tactic T1) (Fig. 3a). In some water bodies, decreased groundwater enhanced nutrient availability through internal eutrophication, making the habitat more favourable for species that can rapidly increase in numbers, such as species of tactic R3, which is mainly represented by the crustacean *Asellus aquaticus*. In other water bodies, conditions have -at least periodically- become harsher as decreased groundwater caused a higher acidity and reduced decomposition rates, or led to water stagnation and hypoxia. Here, insect taxa that could exploit short favourable periods through a short rapid reproduction and avoid unfavourable periods by dispersal (tactic R1), or insect taxa which could tolerate the hardship (tactic T1) increased in numbers. The crustacean *Asellus aquaticus* can exploit fluctuating conditions by spreading reproductive efforts over a long period, but cannot tolerate harsh periods because it is intolerant to low pH and lacks

dispersal or a resistant stage. Thus, not all three tactics increased in each water body of type 2-, but rather one or two of them increased, depending on how environmental conditions had changed. The changes in tactic composition observed in water bodies of type 2- mirror those of water bodies of type 2+, where groundwater influence increased. Here, species of tactic T1, R1 and R3 decreased (Fig. 3a). Increased groundwater probably led to more benign conditions for at least a short, predictable period, causing species with a synchronised life cycle (tactic S1, S2, S3 & S4) to increase. Additionally, species with an asexual reproduction (tactic T2 & R4) can rapidly increase in numbers and respond to this short suitable period.

Changed bog pools, where groundwater influence decreased (type 3-) showed an increase of species with a high tolerance for unfavourable conditions (tactic T1) (Fig. 3b). As species from tactic T1 are capable of active dispersal, their success in these changed water bodies may explain their slight increase in (nearby) unchanged bog pools (type 1 bog pools; Table 4). Elevated water tables in water bodies with decreased groundwater probably increased hypoxia and reduced the occurrence of drought during summer. As a result, species with a long period of juvenile development and lacking adaptations to cope with these harsher conditions (tactic S1) decreased. In addition, species with a synchronised short reproduction period in early spring and a resistant stage (tactic S2) to bridge drought during summer decreased (Fig. 3a). In bog pools where groundwater influence increased, changes in environmental conditions and changes in tactic composition were smaller.
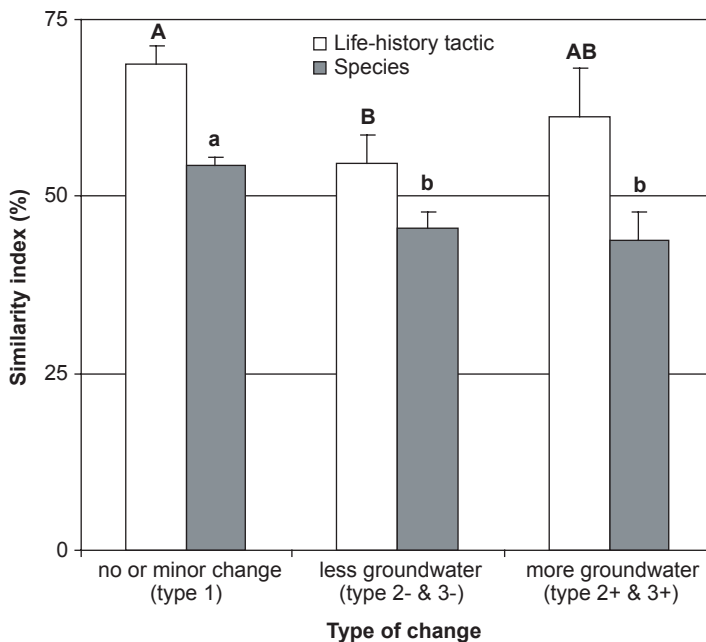
Figure 4 Similarity between a location before and after the execution of the measures. Similarities are presented for tactic composition (Bray Curtis index, on abundance of aquatic macroinvertebrates) and species composition (Sørensen index, on presence-absence of aquatic macroinvertebrate species). Similarities are averaged over locations which have undergone the same type of change. Different letters indicate significant difference ($P<0.05$; Tukey posthoc test, following a separate one-way ANOVA for species and tactics).

Table 4 The percentual composition of life-history tactics averaged over different water bodies. Water bodies are grouped by type of change, with unchanged water bodies subdivided to mesotrophic water bodies, water bodies in wet forests and bog pools. The number of species representing each tactic in a group of water bodies is given between brackets.

Type of change	Before/After measures	Life-history tactic (% abundance)												
		R1	R2	R3	R4	D1	D2	D3	S1	S2	S3	S4	T1	T2
1 mesotrophic waters	B	2.0 (16)	0.6 (2)	12 (1)	8.4 (6)	11.5 (33)	12.6 (4)	0.7 (7)	17.6 (12)	0.8 (10)	0.7 (13)	0.2 (6)	29.5 (43)	3.4 (3)
no or minor changes	A	3.6 (23)	0.6 (3)	12.8 (1)	7.0 (6)	8.5 (40)	21.1 (4)	1.8 (6)	15.6 (16)	1.5 (12)	1.0 (12)	0.1 (1)	22.9 (45)	3.4 (3)
1 wet forests	B	11.1 (16)	<0.1 (2)	48.2 (2)	1.5 (4)	6.3 (12)	-	2.8 (4)	9.4 (8)	1.0 (7)	0.7 (7)	1.3 (3)	12.1 (14)	5.6 (5)
no or minor changes	A	2.9 (10)	0.3 (1)	47.8 (1)	0.5 (4)	2.2 (12)	0.1 (1)	1.5 (5)	9.4 (7)	6.6 (11)	0.6 (7)	0.7 (2)	18.2 (16)	9.3 (4)
2-wet forests	B	2.9 (18)	0.9 (4)	25.6 (3)	5.5 (8)	7.8 (26)	3.9 (2)	1.4 (5)	10.1 (15)	2.8 (17)	3.3 (14)	0.4 (5)	21.7 (26)	13.7 (5)
less groundwater	A	4.7 (22)	1.0 (4)	37.9 (1)	6.1 (6)	2.6 (24)	0.4 (2)	1.4 (6)	8.5 (13)	4.7 (12)	2.9 (17)	0.3 (2)	26.2 (27)	3.4 (4)
2+ wet forests	B	0.7 (5)	0.2 (2)	52.9 (1)	0.3 (3)	7.5 (8)	0.8 (1)	0.9 (3)	2.4 (6)	0.2 (4)	1.4 (2)	1.5 (3)	18.9 (12)	12.4 (3)
more groundwater	A	0.5 (4)	0.5 (3)	50.2 (1)	6 (2)	2.5 (11)	0.4 (3)	0.2 (1)	1.7 (8)	4.0 (6)	2.3 (6)	4.4 (4)	7.4 (15)	20.1 (3)
1 bog pools	B	5.2 (10)	-	0.2 (2)	<0.1 (1)	8.5 (18)	-	1.2 (4)	11.8 (7)	0.9 (8)	5.2 (8)	0.1 (1)	65.6 (25)	1.2 (3)
no or minor changes	A	3.1 (10)	-	<0.1 (1)	-	4.3 (17)	0.2 (1)	0.2 (2)	7.6 (8)	1.2 (7)	5.1 (8)	0.2 (3)	75.3 (25)	2.8 (3)
3- bog pools	B	4.2 (13)	0.1 (1)	5.9 (1)	3.9 (4)	10 (17)	0.3 (2)	1.3 (5)	16.1 (14)	3.2 (10)	5.1 (9)	0.4 (2)	35.4 (22)	14.1 (4)
less groundwater	A	2.4 (13)	-	5.5 (1)	4.4 (2)	9.2 (14)	0.2 (2)	0.3 (3)	3.1 (7)	0.3 (7)	5.6 (8)	0.2 (2)	58.1 (24)	10.6 (3)

In water bodies that were not affected by the restoration measures (type 1), tactic composition remained fairly constant, with the exception of some water bodies in wet forests, where species of tactic S2 increased and species of tactic R1 decreased.

When summarising the changes in life-history tactic composition in a similarity index (Fig. 4), changes in unchanged water bodies (type 1) were smaller compared to water bodies with a decrease in groundwater influence and higher water tables (type 2- and 3-). This indicates that the strongest functional shifts have occurred in the latter water bodies. The functional shifts in water bodies with an increase in groundwater (type 2+ and 3+) did not differ from unchanged water bodies. However, regarding changes in species composition (Fig. 4), all changed water bodies showed larger changes (lower similarity) compared to unchanged water bodies (type 1).

The average similarity of water bodies located within the same compartment increased significantly by 8.7%, becoming more similar in life-history tactic composition following rewetting measures (Fig. 5). For reasons of comparison, water bodies of the same water type were on average 15.4 % more similar compared to water bodies of a different water type (based on data from the first sample period before measures were taken). Increases were largest for compartments 1 and 2, followed by compartment 5 and 6, corresponding to the compartments where rewetting took place. These results indicate that within-compartment variation in environmental conditions, relevant to aquatic invertebrates, declined after restoration measures were taken. This is also reflected in lower cumulative numbers of species for compartments 1 and 2 (Fig. 6).

Species turnover was related to the effect of restoration measures as expressed in type of change (Fig. 7). Average number of species gained is mostly equal or slightly higher than the average number of species lost. However, the cumulative number of species gained and lost, differs between the different types of change. More species are
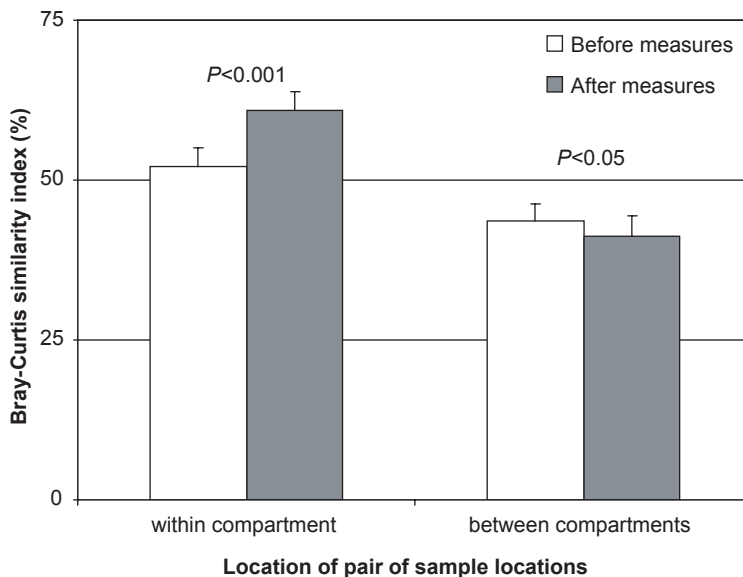
Figure 5 Average similarity (+ standard error) in life-history tactic composition between pairs of water bodies located within the same compartment and in a different compartment (different compartments are indicated in figure 2) both before and after the execution of rewetting measures.
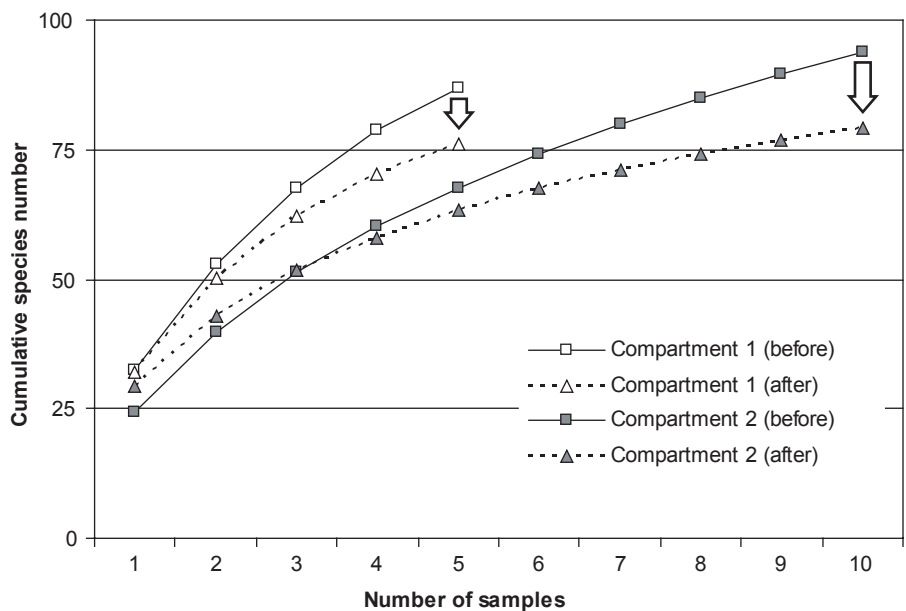
Figure 6 Species accumulation curves for compartment 1 and 2 where most extensive rewetting was realized.

gained than lost in water bodies with an increase in groundwater influence (type 2+ and 3+). In contrast, more species are lost than gained in water bodies with less groundwater influence and higher water tables (type 2- and 3-), which is especially evident in type 3-. Here, the same species are gained at various water bodies, but at each water body, different species are lost, resulting in a lower cumulative number of species.
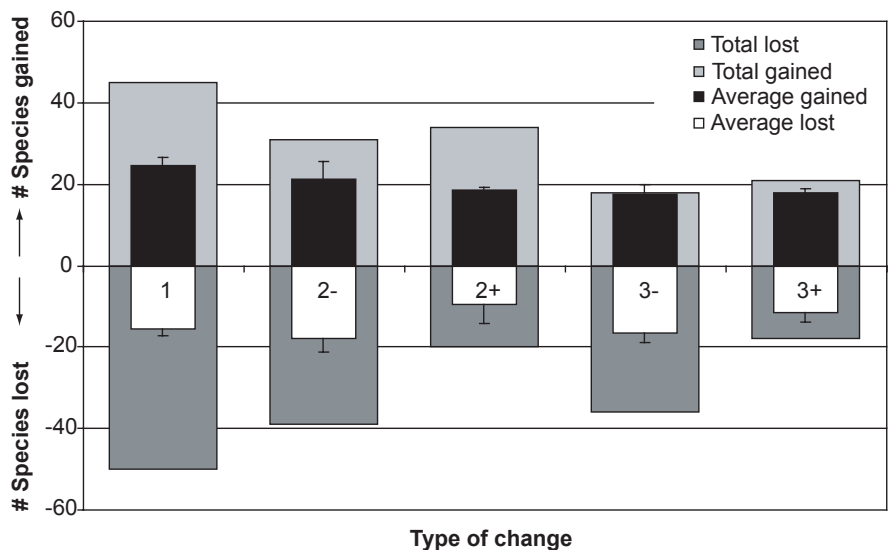
Figure 7 Average and cumulative species turnover for each type of change. See table 2 for an overview of the different types of change.

Discussion

Life-history tactics as a tool

Measuring restoration at the community level is complicated due to the high variability of communities. Palmer *et al.* (1997) suggest that a focus on restoration of functional groups, rather than on particular species is more appropriate. In our study we used life-history tactics as a tool to determine whether changes in species composition were related to the effects of the restoration measures. Changes in tactic composition could be related to changes in environmental conditions through mechanistic explanations, based on a species' capabilities and constraints derived from combinations of its species traits. In this way the response of aquatic macroinvertebrates could be functionally interpreted. Decreased groundwater caused fluctuations in environmental conditions with periods of harsher conditions (*e.g.* higher acidity, periodic low oxygen or lower decomposition rate). This resulted in the increase of both tolerant species (tactic T1) and species that spread their reproductive effort in time, space or both (tactics R1 & R3). Increased groundwater retained (bog pools) or increased (wet forests) predictable conditions, which promoted species with a synchronised life cycle (tactics S1, S2, S3 & S4). Thus, tactic composition varied consistently with changes in groundwater and changes in tactic composition were similar for both types of changed water bodies.

Life-history tactics may also explain changes that are not related to effects of restoration measures. For example, changes in tactic composition in unchanged water bodies in wet forests probably reflects the extremely dry summer conditions in 2003. Summer drought has probably constrained reproduction of mobile species with successive reproduction events spread over a long period (tactic R1), and increased reproductive success of species with a synchronised short larval development and resistant stages (tactic S2). Indeed, these changes in tactic composition occurred primarily in two water bodies of wet forests, which were both prone to drying out. Moreover, the facilitating effect of summer drought in 2003 on species from tactic S2 is expected to be diminished in rewetted locations, most so in places where the water table has increased (type 2-), which is confirmed by the data (Table 4).

Effects of restoration measures

Effects of the restoration measures strongly depended on the type of measure. The construction of dams and retention of rainwater led to a rapid (usually within a year) and substantial increase (frequently up to 50 cm) in the water table within large parts of a compartment, decreasing the influence of groundwater. This constituted a major impact, causing the die-off of *Betula* trees in rewetted parts. Retention of rainwater may also have acted as a shock effect for macroinvertebrates, because for water bodies where groundwater influence decreased, changes in tactic composition were largest (Fig. 4), and species losses exceeded species gains (Fig. 7). Alternatively, reduced drainage and increased infiltration resulting from filling of drainage ditches locally increased groundwater influence. These changes were more gradual for aquatic macroinvertebrates as changes in tactic composition did not differ from those in unchanged water bodies (Fig. 4) and species gains exceeded species losses (Fig. 7).

In rewetted compartments environmental heterogeneity declined, as indicated by an increased similarity in tactic composition between water bodies in the same compartment (Fig. 5). Rewetting may act as a species filter (Poff 1997; van Kleef *et al.* 2006), promoting

the expansion of a few life-history tactics at all water bodies within a compartment, while constraining the other tactics. This resulted in a decrease of cumulative numbers of species (Fig. 6). Although the process of bog restoration will take much longer than the period studied here, this study shows that in a two year period, species belonging to several different life-history tactics are susceptible to going locally extinct as shock effects and homogenisation results in a loss of suitable conditions. The potential for successful restoration of animal diversity may be markedly decreased if species are lost in the short term, as recolonisation may proceed very slowly (van Duinen *et al.* 2003; 2007).

Implications for restoration management
Improving the effectivity of restoration management requires a framework of causal mechanisms (Bradshaw 1996; Jansson *et al.* 2005). Such a framework may explain how the system naturally functions, how it is impacted and how it can be restored (Hobbs & Norton 1996; Brouwer *et al.* 2005). Figure 8 gives a schematic representation of the structure and function of an ecosystem in different states (intact, degraded, restored). In pristine bog landscapes, structure and function are strongly connected. In the raised bog centre, the growth of the ecosystem engineer *Sphagnum* gives rise to a pattern of hummocks and hollows (van Breemen 1995; Couwenberg & Joosten 2005). Supply of minerotrophic ground- and surface water creates lagg zones and transitional mires. These parts of the bog landscape are hot spots for many species, which are nowadays threatened (Schouwenaars *et al.* 2002; Schouten 2002; Smits *et al.* 2002; van Duinen *et al.* 2006).

Impacts of degradation extent further than desiccation. Peat cutting and land cultivation started from the edges and led to the complete disappearance of a lagg zone and transitional mire in most bog remnants. In the centre, peat cutting damaged or
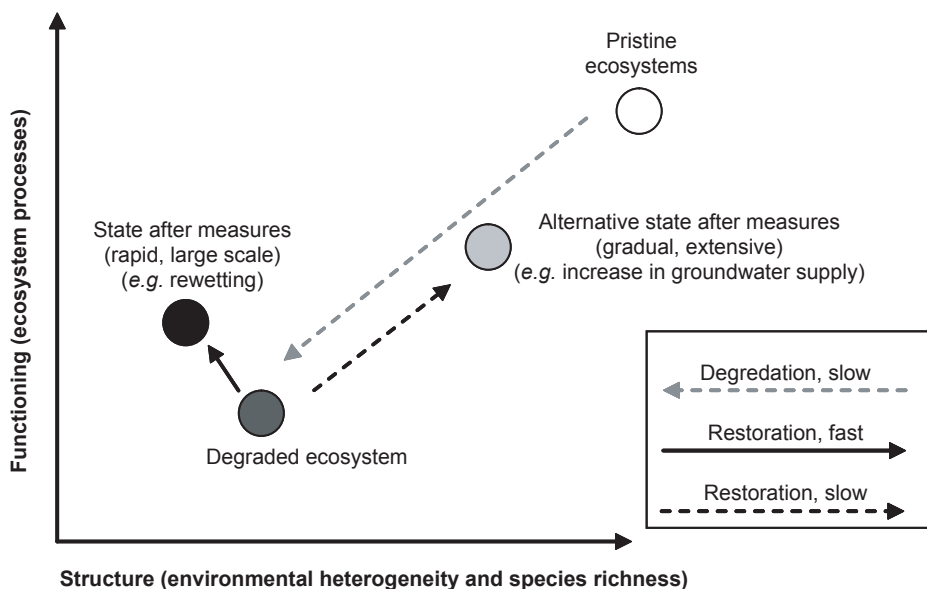

Figure 8 Schematic representation of the changes in structure and functioning in raised bog ecosystems following degradation, current rewetting practice and the proposed alternative, involving restoration of the regional hydrology. Modified from Bradshaw (1996).

destroyed the acrotelm layer, reducing the water retention capacity. Drainage reduced supply of minerotrophic groundwater. Finally, increased nutrient availability has led to the expansion of *Molinia caerulea* and *Betula* sp. (Tomassen *et al.* 2004). All these changes have reduced both structure and functioning (Fig. 8), contributing to desiccation in different ways, reducing supply of minerotrophic water and increasing nutrient availability.

Because desiccation is but one aspect of the problem, water retention is but one aspect of the solution. Rewetting by retaining rainwater may partly ameliorate desiccation in the centre stimulating processes such as *Sphagnum* growth, but supply of groundwater is not restored or may further decrease. In addition, results show that large-scale rewetting may further reduce environmental heterogeneity. The consequence for aquatic macroinvertebrates is that relevant environmental heterogeneity is lost (Fig. 5; Chapter 1), resulting in a decline of cumulative species numbers within rewetted compartments (Fig. 6). Thus, large-scale rewetting may partly restore processes but involves a further loss of structure (Fig. 8). Consequently, the preservation and if possible strengthening of heterogeneity constitutes a more effective restoration management. This can be best achieved by strengthening the natural processes underlying heterogeneity (Palmer *et al.* 1997; Dobson *et al.* 1997).

The supply of minerotrophic (ground)water is a key process in bog landscapes, as the majority of bogs have developed by transitions from minerotrophic to acidic peatlands (Lamers *et al.* 1999). Also secondary succession may depend on groundwater as minerotrophic groundwater in the base of the peat substratum may stimulate formation of CO_2 and CH_4 (Lamers *et al.* 1999), which is subsequently incorporated in *Sphagnum* (Raghoebarsing *et al.* 2005). Therefore, increasing the supply of minerotrophic (ground)water constitutes a more promising restoration strategy than large-scale rewetting (Fig. 8). This will also be beneficial for aquatic macroinvertebrates. On the short term, improvements will be gradual allowing species to redistribute in response to the changed environmental conditions (van Duinen *et al.* 2004), and on the long term environmental heterogeneity will increase. Increasing the supply of minerotrophic (ground)water can be achieved by improving the regional hydrology and reducing local drainage. This may require extensification of land use in the surrounding landscape and the creation of a hydrological buffer zone. These measures aimed at the regional hydrology may be supplemented by small scale measures to remove acute, internal barriers to ecosystem recovery or prevent risks of local species extinction (*e.g.* locally stemming water run-off or logging of trees).

In restoration ecology the focus is on vegetation and it has been argued that this is just, as 'plants comprise the *vast majority* of all terrestrial ecosystems' biomass, and anchor the base of trophic pyramids' (Young 2000). While we acknowledge this point, we caution against taking measures primarily from a botanical viewpoint, measuring success by the return of focal plant species. With animals and especially invertebrates comprising the *vast majority* of all species, their return will ultimately indicate successful restoration of ecosystem functioning *and* ecosystem structure.

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A glanville fritillary (Melitaea cinxia) sitting on brown knapweed (Centaurea jacea). Photo: Wilco Verberk.

Chapter 7

Synthesis

Verberk WCEP

Development of life-history tactics

Unravelling the relationship -or '*match*'- between a species and its environment requires knowledge on both (Fig. 2 in Chapter 1). Which problems and opportunities for a species are present in an environment and what are strengths and weaknesses of the species in that environment?

Chapter 2 focuses on variation in environmental conditions and describes the result of a comparative field survey. Different species were captured in each sampled water body and this variation in species composition could be related to differences in environmental conditions. Scatter is frequently observed around species-environment relationships and may arise from different sources of variation. Adjacent water bodies were more alike with respect to species assemblage than expected from the differences in environmental conditions, indicating that spatial configuration plays a role in the exchange of individuals. Other factors contributing to scatter around the species-environment relationship are related to natural dynamics and sampling. For example, environmental conditions may have become recently suitable but the species has not yet colonised, or a species may have been missed during sampling, merely appearing to be absent (Niggebrugge *et al.* 2007). Due to these sources of variation and different methods for analysing species-environment relationships, different results can be obtained with little indications for which result best reflects reality (Nijboer 2006). Although it may be important in generating hypotheses, successfully relating species and environmental conditions statistically does not provide explanations. This requires information on the life-history of a species.

Chapter 3 focuses on differences in species traits between aquatic macroinvertebrate species. Because species traits determine a species' ability to deal with environmental problems and opportunities, they can potentially be used to explain a species' occurrence under particular environmental conditions (*e.g.* Keddy 1992; McGill *et al.* 2006; Nijboer 2006). These species traits were interrelated and their function for a species' survival was context-dependent, being related to the remainder of a species' basic morphology (Gould & Lewontin 1979). Thirteen different life-history tactics were defined, based on combinations of species traits and their function.

In Chapter 4 the water types described in Chapter 2 are characterised in terms of the abundance of species belonging to the various life-history tactics. This provided information on how the various water types are experienced by the species present. In this way, life-history tactics provided plausible links between two data-sets of different origin, with on the one hand data from literature on the biology of the various species (condensed in life-history tactics in Chapter 3) and on the other hand field data on both species occurrences and environmental conditions (Chapter 2).

Strengths and weaknesses of life-history tactics

Analysing species-environment relationships from a life-history tactic approach has several strong points and a few weak points (Table 1). These strengths and weaknesses pertain to causality and aggregation. They will each be discussed separately, although in fact they are intimately related.

Table 1 Overview of strong and weak points pertaining to the causality (C) or aggregation (A) of life-history tactics.

Strong points	Weak points
incorporates a species' natural history (C)	detailed knowledge on species' biology required (C & A)
based on causal mechanisms (C)	no fixed guidelines for trait function (C & A)
generates testable predictions (C)	no fixed criteria for level of aggregating (A)
new species may be added relatively simply (A)	
reduces complexity (A)	

Causality

The core of the life-history tactic approach is that separate traits are combined to 'sets of co-adapted species traits designed, by natural selection, to solve particular ecological problems' (Stearns 1976). Therefore, in life-history tactics, interrelations between species traits and interpreting the function of trait combinations are taken as a starting point. Life-history tactics incorporate the causal mechanisms for a species' survival under particular environmental conditions, as they are based on species traits related to the reproduction, development and dispersal of a species and synchronisation thereof (Chapter 3). This allows the explanation of differences in species assemblages between locations or periods, provided that the main causal mechanisms are included.

The drawback is that for defining life-history tactics, detailed knowledge is required on (i) the traits possessed by a species, (ii) interrelations between these traits, (iii) and how the functional relevance of such trait combinations should be interpreted. Given the huge range of species traits, there are no fixed guidelines for how to interpret the function of traits or combinations of traits. Consequently, such interpretations may be criticised for being subjective and lacking scientific rigour. This makes it difficult to make the concept of traits operational so that it may be applied and may well explain why the rich body of literature on the natural history of many species has been largely ignored in community ecology. By rooting interpretations in fundamental trade-offs known from life-history theory and by viewing trait combinations as a part of the entire organism's biology (Gould & Lewontin 1979), subjectivity in interpreting the function of combinations of species traits was minimised (Chapter 3). Taking the function of species trait combinations in account presents an advantage to multivariate analysis techniques and the use of phylogenetic independent contrasts. In these other methods, species traits are treated as functionally equivalent (*e.g.* Resh *et al*. 1994) or species traits both with and without a clear function are controlled for if they are related to a species' phylogeny (*e.g.* Felsenstein 1985).

In short, life-history tactics allow information on the natural history of a species to be integrated in community ecology to derive the most likely explanations and generate testable predictions. In Chapter 5, information on the reproduction and dispersal of species (condensed in life-history tactics) was used to predict if and how a species would deviate from the general observed pattern that locally abundant species are widely distributed and vice versa. Predictions were significantly related to observations, providing evidence that the causal mechanisms that are most likely to facilitate or constrain species on a local and regional scale were incorporated in the life-history tactics. By providing the most likely explanations -or by challenging previously held notions- life-history tactics may focus subsequent research and management efforts. Further research may focus on

obtaining more information on species traits or on expanding the life-history tactics to include other species groups and ecosystems, such as aquatic macroinvertebrates from lotic waters and waters with fish.

Aggregation

Theoretically, species traits can be combined in an almost infinite number of ways. For example, 15 different traits with each three modalities (for instance being absent, weakly developed or strongly developed) already yields 14,348,907 combinations (315). In reality, species traits proved to be strongly interrelated, greatly reducing the number of combinations possible (Chapter 3). Therefore, once life-history tactics are developed, new species may be added relatively simple; exhaustive data on every aspect of a species' biology does not seem necessary, rather information on a number of key traits is sufficient to assign a species to a certain tactic.

The number of trait combinations is further reduced in life-history tactics by recognising that certain trait combinations may be functionally equivalent: species may possess different combinations of species traits, for instance due to differences in basic morphology, but different trait combinations can solve the same environmental problem (Koehl 1996). Species identification will remain necessary for assigning species to a certain tactic. Nevertheless, life-history tactics reduce assemblages of many species belonging to many different systematic groups to a small number of tactics, representing meaningful and interpretable relationships between species and their environment (Chapter 4).

By grouping species in life-history tactics, the signal to noise ratio increases when differences, which may be regarded as noise are aggregated while relevant differences are kept separated. An example of 'aggregating noise' is given in Chapter 4 for different types of bog pools. These bog pools were similar with respect to being acid and nutrient poor. Although partly represented by different species in each type of bog pool, species with a high tolerance for unfavourable conditions (tactic T1) were abundant in all three types of bog pools (Fig. 5 in Chapter 4). An example of 'keeping relevant differences separated' is given in Chapter 6, where species assemblages were studied before and after restoration measures were taken. Changes in average number of species did not differ much between water bodies where groundwater influence had increased and those where groundwater influence had decreased. In contrast, changes in tactic composition revealed a clear difference between increased or decreased groundwater influence and this difference was consistent over the different water types affected (bog pools and wet forests).

Determining what level of aggregation is most appropriate presents a problem when grouping species. Although it is impossible to give fixed criteria, ideally the level of aggregation should strike a bargain between maximising the signal while at the same time minimising the noise. Therefore, the appropriate level of aggregation depends on both the range in interspecific biological differences and the range in environmental conditions. Thus, when considering a single systematic group, or a narrower range in environmental conditions, species groups may be further refined to achieve a higher resolution. For example, in their study on the response of Chironomidae to natural recovery and recovery following restoration measures in moorland pools, van Kleef *et al.* (in preparation) distinguished six tactics for Chironomidae, rather than the four distinguished here.

Position of life-history tactics in community ecology

Community ecology searches for general rules to explain patterns in species' distribution, but to date, progress has been slow (Keddy 1992; Weiner 1995; Lawton 1999; McGill *et al.* 2006). This lack of progress has been explained by the fact that ecological rules - and the mechanisms that underpin them - are contingent on the organisms involved, and their environment (Lawton 1999; Simberloff 2004). Coupled with the vast complexity of biological systems, the result is that there are few rules that are universally true in community ecology. Life-history tactics are here positioned within in the field of community ecology, which is best envisaged as a continuum. The merits of the life-history tactics are compared with two approaches in community ecology, which can be considered the end points of this continuum, focussing either on individual species or aggregating information spanning multiple species (Table 2).

Table 2 Causality and aggregation of species approach, life-history tactic approach and community approach. The different approaches are visualised in figure 1 and further explained in the text.

Strong points	Species approach	Life-history tactic approach	Community approach
Aggregation	-	++	+++
Causality	+++	++	-

Species approach and community approach
When focussing on a single or a few species, information on the causal mechanisms, which are derived from the environmental context and a species' natural history, is used to explain a species' success. The drawback of a species approach is that the results are difficult to generalise to other communities, consisting of other species. By simplifying the complexity, information spanning multiple species can be aggregated, thus enabling different communities to be compared. Examples of aggregated community attributes include various indices (*e.g.* diversity, eveness and similarity indices) and plots (*e.g.* rank abundance plots, species accumulation curves). Such an approach treats communities as a frequency distribution of index scores and ignores a species' rich natural history. In effect, species are treated as faceless entities and communities as black boxes, which may explain the success of neutral theory in accurately describing communities in terms of indices of aggregated information (Bell 2001; Chave 2004). The focus on aggregated community attributes in the community approach obscures the causal mechanisms. This hampers scientific understanding, which ultimately comes from explanations based on causal mechanisms (Weiner 1995). For example, a correlation between the species diversity and the primary productivity (*e.g.* Waide *et al.* 1999), does not explain why certain species go extinct nor does it allow predictions concerning the fate of the remaining species. Consequently, its use for application to any specific situation is limited, as specific environmental conditions and the associated species, may represent exceptions to the observed pattern. The heart of the problem is that environmental conditions are used to explain the aggregated information spanning multiple species, while in fact explanations are species specific. In other words, there is a mismatch between the phenomenon to be explained and the level of causation. Therefore, simplifying the complex reality for reasons of comparison, may be the cause, rather than the cure for the lack of progress in community ecology.

Life-history tactics

Life-history tactics may provide the best of both worlds, aggregation information over many different species without sacrificing information on the causal mechanisms underlying a species' presence or absence (Table 2). Figure 1 visualises the differences between the life-history tactics and the species approach. When focussing on individual species, it is difficult to judge the importance of the various causal mechanisms relating a species' occurrence to its environment, as there is no point of reference (*i.e.* other species). Causal mechanisms act through species traits, which together with the spatial and temporal variation in environmental conditions (including both abiotic and biotic factors) determine the suitability and connectivity of the environment from that species' point of view. Life-history tactics represent a species' integrated response to the environment as many traits are jointly considered. Furthermore, interspecific differences in such responses are incorporated in life-history tactics. This provides the contrasts, which are necessary to ascertain which set of causal mechanisms are most important for a given group of species in the environment under study.
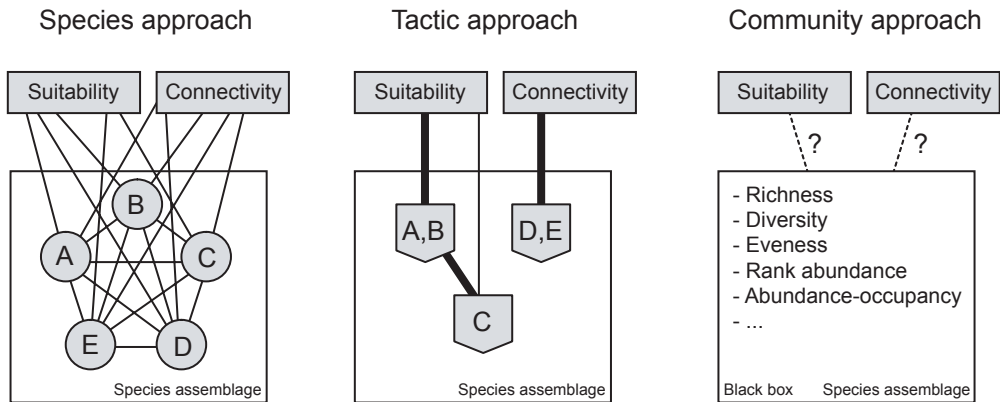
Figure 1 Visualisation of the differences between life-history tactics, the species approach and the community approach. In the species approach causal mechanisms are not differentiated in importance. With life-history tactics, species are grouped and the most important causal mechanisms are shown for a given species group. In the community approach, information spanning multiple species is aggregated, obscuring the causal mechanisms. See text for further explanation.

Life-history tactics and macroecology

Life-history tactics may be used in further research to provide insight into the causal mechanisms underpinning statistical patterns involving large sets of species. By taking many different species into account, the variation resulting from contingency is averaged out and broad statistical generalisations have been found, including for example allometric relationships (Hendriks 1999) and relationships between abundance and occupancy (Brown 1984). Life-history tactics may explain a significant part of the scatter around the observed generalisation, as was shown for the relationship between abundance and occupancy in Chapter 5. Similarly, strong allometric relationships are found for reproduction rate or life span, while relationships are more variable for a species' density or territory size (Hendriks 2007). The density of a species or the size of its territory typically results from the interplay between the prevailing environmental conditions and

various species traits. Relationships between these species traits and body mass may differ between species. For example, body mass is a poor predictor for development time in species with a larval diapause. Life-history tactics may improve allometric relationships by providing insight in how body mass affects other species traits for a given life-history tactic.

Merits of life-history tactics in restoration ecology

A clear understanding of the functioning of the system of interest and changes therein due to anthropogenic impacts is vital for the effectiveness of restoration management. Such an understanding requires a framework of causal mechanisms (Bradshaw 1996; Jansson *et al.* 2005), which may explain how the system naturally functions, how it is impacted and how it can be restored (Hobbs & Norton 1996; Brouwer *et al.* 2005). Thus achieving the goals set in community ecology is what is required for effective restoration management (Palmer *et al.* 1997), blurring the line between fundamental and applied research. Therefore, the problems in community ecology also hamper restoration ecology. For the use of macroinvertebrates in ecological assessment and biomonitoring, water managers have a wide variety of tools at their disposal, ranging from simple diversity indices to complex methods (Verdonschot 2000). However, the complex methods (*e.g.* multivariate analysis techniques) used in ecological assessment and biomonitoring may lead to different conclusions, depending on subjective choices made during the data analysis (Nijboer 2006). These complex methods generate large amounts of information (*e.g.* multimetrics), making it difficult to identify key mechanistic explanations underpinning patterns in species occurrence (lack of aggregation), while aggregating information into single indices does not incorporate the causal mechanisms (lack of causality) (Chapter 4).

In this thesis, life-history tactics for aquatic macroinvertebrates were developed and applied. Chapter 4 has demonstrated that the identity of the tactics, their numerical dominance and their co-occurrence with other tactics provides insight in how the different water types functions for the species present. An understanding of the functioning of the system may explain why current restoration practices are not or only partially successful and may provide handholds for alternative, more promising ways to achieve restoration. For example, in Chapter 6, life-history tactics were used to relate changes in species composition to the effects of restoration measures in a bog remnant. Water retention favoured species that were adapted to unpredictable conditions (tactics R1 & R3 in Chapter 3), while species adapted to more stable and predictable conditions (tactics S1, S2, S3 & S4 in Chapter 3) were constrained. More general, the negative effects of desiccation are not remedied by large scale rewetting, because both degradation and large scale restoration result in a loss of environmental heterogeneity (Chapter 6). Life-history tactics have also been successfully applied to other species and other systems, including soil arthropods (Siepel 1995) and ants in chalk grasslands (van Noordwijk *et al.* in preparation). Life-history tactics may thus present a useful tool to evaluate and direct restoration management.

The relation between heterogeneity and species diversity
Environmental heterogeneity is associated with a high species diversity in many terrestrial and aquatic habitats (*e.g.* Huston 1994; Heino 2000; Kerr *et al.* 2001; Chapter 2). However, what constitutes a heterogeneous environment depends on the species in question, governing the appropriate scale level and environmental factors. This may explain why attempts to formulate general mechanisms underlying the observed relationship have been largely restricted to theoretical models. Theoretical models reduce the issue to a problem of coexistence and formulate ways in which environmental heterogeneity can prevent competitive exclusion (*e.g.* Tilman 1994; McPeek 1996; Chesson 2000; Amarasekare 2003). Theoretically, two species can coexist if both species can maintain positive growth when they are least abundant, which requires intraspecific competition to outweigh interspecific competition (Chesson 2000).

In addition, heterogeneous landscapes (*i.e.* those with a combination of different parts) may harbour more species compared to the 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. Explanations for the occurrence of these additional species in heterogeneous landscapes are given in chapter 2 with species (i) requiring certain conditions which only occur in a gradient between two different habitat types, (ii) depending on a combination of two or more different habitat types, and (iii) being able to better persist.

The life-history tactic of a species gives information on the likely importance of each of the above explanations. The first explanation (gradient conditions) is a likely candidate for species with a long juvenile growth period (for stable gradients) and/or a high degree of synchronisation (for predictable gradients), for example tactics S1, S4 and T1 listed in Chapter 3. The second explanation (multihabitat use) is a likely candidate for species with an active dispersal, having a short juvenile growth period, and/or (relatively) longlived adults, for example tactics S2 and R1 listed in Chapter 3. The third explanation (higher persistence) is a likely candidate for species with a high dispersal and a high reproduction rate, such as tactics D1, D2 and D3 listed in Chapter 3. Especially semelparous species with high numbers of eggs are expected to achieve high persistence by avoiding competition through strong aggregation (Shorrocks *et al.* 1984), such as for example chironomids of tactic D3.

Restoration of heterogeneous and biodiverse ecosystems
Species are not only passengers, but can also be drivers (sensu Walker 1992). Species aggregate and store resources, depriving other nearby patches from a similar supply. This retention results in decreasing temporal variation (variability) and increasing spatial variation, creating patterns (Rietkerk *et al.* 2002), such as the hummock-hollow structure of a raised bog (Couwenberg & Joosten 2005). In turn, this may promote biodiversity on an ecological timescale, through a further partitioning of the environment in space or by allowing the build up of sufficient population size in between disturbance events. In short, biodiversity begets biodiversity, which has been reported for a range of ecosystems (Estes *et al.* 1978; Knops *et al.* 1999; Ritchie & Olff 1999; Janz *et al.* 2006).

Given the intimate links between species diversity and environmental heterogeneity, it is apparent that environmental heterogeneity plays an important role in the conservation of biodiversity. Environmental heterogeneity is the result of many individuals of many species growing, reproducing and dying (generally living their lives), thus interacting with their surroundings and in the process aggregating, redistributing resources, modifying

ecosystem processes, thus shaping the landscape into a mosaic of different patches and gradual transitions in between (Baaijens 1985). Therefore, restoring heterogeneity directly is difficult. Rather, the restoration of the natural processes driving heterogeneity will often be the best option. This may require the restoration of abiotic boundary conditions, active species restoration, or both. For example in Chapter 6, results indicate that restoring the regional hydrology offers a more promising restoration strategy in bog landscapes, leading to a gradual improvement of environmental conditions and strengthening of environmental heterogeneity. Further research on bog restoration may characterise a pristine bog landscape in terms of life-history tactics. This would enhance our understanding of how different parts of a pristine bog landscape function for aquatic invertebrates and provide additional handholds for restoration. Also in riverine landscapes strengthening environmental heterogeneity requires abiotic boundary conditions to be restored. Here protected and endangered riverine species will benefit from restoration of the spatial gradient in hydrodynamics (Ward *et al.* 1999; de Nooij *et al.* 2006). In contrast, the collapse of many coastal systems is attributed to overfishing, and consequently restoration is most likely to succeed through recovery of fish stocks (Jackson *et al.* 2001). Life-history tactics provide insight in the functioning of ecosystems and may help to unravel the importance of abiotic boundary conditions and species interactions. Successful conservation of biodiversity will strongly depend on this ability to identify and subsequently strengthen the processes underlying landscape heterogeneity.

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Meddose veen in spring (26 July 2001). Photo: Wilco Verberk.

Summary

Human activities profoundly influence our landscapes today. Changes in land use, acidification, desiccation and eutrophication have resulted in a biodiversity crisis. Knowledge on the relationship -or '*match*'- between a species and its environment is needed to understand the impact of degradation and to derive sound possibilities for restoring the original biodiversity.

This issue was addressed in a case study on the aquatic macroinvertebrates in lentic freshwater habitats of the Korenburgerveen, a heterogeneous bog remnant located in the east of the Netherlands. **Chapter 1** provides a short introduction to the problem of scale and the match between a species and its environment, giving rise to central question of this thesis: "How to make sense of the large variety in species-environment relationships?" To match species to changing landscapes requires the development, application and evaluation of a method by which relationships between aquatic macroinvertebrate species and their environment can be explained and aggregated to a manageable number of key relationships. This is the main goal of this thesis.

To relate species composition and species richness to environmental conditions, the species assemblages of Korenburgerveen were compared with those of six other bog remnants in the Netherlands. The results of this field survey are described in **Chapter 2**. Aquatic invertebrate species in bog remnants may depend on the environmental heterogeneity. For example, different water bodies, or different parts of a water body, are required for hibernating, foraging and the reproduction of a species. In addition, degrading effects of acidification, desiccation and eutrophication decrease environmental heterogeneity by causing persistent and similar changes over large areas. Therefore, the relation between environmental heterogeneity and species diversity was studied in detail. Species diversity was higher in bog pools situated in a heterogeneous landscape, compared to bog pools situated in a more homogeneous landscape. In addition, variation in species composition was correlated to differences in environmental conditions and spatial configuration. However, such statistical correlations by themselves do not explain species-environment relationships. Explaining such relationships requires the causal mechanisms to be incorporated in the analyses.

To deal with the various problems and opportunities in their environment, species have developed physiological, morphological and behavioural traits in the course of their evolution (*e.g.* a chitinous exoskeleton, diapausing eggs, parental care, large body size and short development time). Therefore, causal mechanisms explaining a species' environmental requirements are rooted in species traits. To use species traits in explaining species-environment relationships, interrelations between species traits and the functional implication of species trait combinations are investigated. The results of this literature study are described in **Chapter 3**. The large variety in species traits presents a problem when trying to group species based on species traits. By investigating how traits are linked through trade-offs and spin-offs the number of trait combinations could be reduced. In addition, from these interrelations the function of trait combinations was interpreted (*e.g.* reduce egg mortality, speed up development, spread risks). In this way, it was possible to define 'sets of co-adapted species traits designed by natural selection to solve particular ecological problems', which are termed life-history tactics. Species with alternative suites of traits that solved environmental problems in a similar way were assigned to the same tactic. This provided a functional classification spanning species from different systematic groups.

In **Chapter 4** water types described in Chapter 2 were characterised in terms of the abundance of species belonging to the various life-history tactics. Differences in tactic composition based on species abundances between the different water types were related to the prevailing environmental conditions governing the duration, degree and predictability of habitat suitability in space and time. For example, species with a long period of juvenile development and a synchronised emergence of short-lived adults were most dominant in large mesotrophic water bodies with stable and predictable environmental conditions. In contrast, species that have a fast development and spread successive reproduction attempts over a longer time period were most abundant in water bodies with fluctuating and less predictable environmental conditions. This demonstrates the value of life-history tactics in providing mechanistic explanations for differences in species assemblages. As such life-history tactics are widely applicable from ecological research to environmental quality assessment programmes. Applying life-history tactics reduces the vast complexity of many species belonging to many different systematic groups to a small number of tactics (although species identification will remain necessary). This allows extrapolation to and comparisons between communities consisting of different species. Life-history tactics were applied to a fundamental and an applied problem in ecology in Chapter 5 and 6.

In **Chapter 5**, the fundamental problem of why locally abundant species are also widely distributed is studied. Such a positive interspecific abundance-occupancy relationship is one of the most robust patterns in macroecology. Predictions whether a species would be relatively abundant or widespread were constructed for each species based on its life-history tactic. Tactics with a clustered oviposition, or a high rate of increase (for instance through asexual reproduction) were relatively abundant, whereas tactics with a high dispersal, or a small clutch size were relatively widespread. Therefore life-history tactics can provide insight into the causal mechanisms underpinning statistical patterns involving large sets of species.

In **Chapter 6**, the applied problem of evaluating the effects of large scale rewetting measures in a bog remnant on aquatic macroinvertebrates is studied. Rewetting was realised by constructing dams to retain rainwater and filling drainage ditches. Retention of rainwater increased water tables and decreased the influence of groundwater, while reduced drainage locally increased groundwater. With the use of life-history tactics, changes in species abundance and composition were related to the effects of restoration measures through mechanistic explanations. Large-scale retention of rainwater was shown to decrease environmental heterogeneity. Therefore, increasing groundwater influence by restoring the regional hydrology is a more promising strategy. Increased supply of minerotrophic groundwater gradually gives rise to stable, minerotrophic transitions, which are important hotspots for biodiversity in pristine raised bog landscapes. Furthermore, this restoration strategy is more in agreement with current views that minerotrophic conditions play a key role in primary and secondary succession in bogs. Restoring such natural processes driving heterogeneity may increase the effectiveness of restoration plans for animals by restoring both ecosystem functioning and structure.

The position of life-history tactics in community ecology and its merits in restoration ecology are discussed in **Chapter 7**. Life-history tactics are based on species traits and therefore integrate information on a species' natural history into community ecology. By including the causal mechanisms for a species' survival under particular environmental conditions, life-history tactics can be used to derive the most likely explanations and

generate testable predictions. This is exemplified in Chapter 5 and 6, where life-history tactics were successfully applied to a fundamental and applied problem in ecology. Life-history tactics can aggregate information over many different species without sacrificing information on the causal mechanisms underlying a species' presence or absence. These properties make life-history tactics ideally suited to fill the gap between a species approach and a community approach in community ecology. In the latter, information spanning multiple species (*e.g.* diversity indices, rank abundance plots) is aggregated, but causal mechanisms are obscured. In the former, causal mechanisms are included, but their relative importance is unknown and consequently aggregation is difficult. By incorporating causal mechanisms, life-history tactics may complement research efforts in macroecology (Chapter 5).

Given the intimate links between species diversity and environmental heterogeneity, it is apparent that environmental heterogeneity plays an important role in the conservation of biodiversity. Environmental heterogeneity results from the interplay between abiotic conditions and the effect of many individuals of many species. Therefore, restoring heterogeneity directly is difficult. Rather, the restoration of the natural processes driving heterogeneity will often be the best option. This may require restoration of abiotic boundary conditions, restoration focussed on particular species, or both. Life-history tactics provide insight in the functioning of ecosystems and may help to unravel the importance of abiotic boundary conditions and species interactions. Successful conservation of biodiversity will strongly depend on this ability to identify and subsequently strengthen the processes underlying landscape heterogeneity.

The main conclusions of the research presented in this thesis:
- Heterogeneous bog landscapes have a higher diversity than more homogeneous ones. A higher diversity can be explained by heterogeneity facilitating species that depend on a combination of habitat types, or on gradient conditions formed between different habitat types, or by heterogeneity increasing a species' persistence.
- Species traits are strongly interrelated through trade-offs and spin-offs. A functional interpretation of trait combinations in life-history tactics allows a coherent synthesis of biological differences between aquatic macroinvertebrates belonging to different systematic groups.
- Life-history tactics are based on species traits and consequently incorporate the causal mechanisms underlying the relationship -or '*match*'- between a species and its environment. Therefore they can be used to derive the most likely explanations and generate testable predictions. As such life-history tactics can be applied as a tool for ecological assessments and biomonitoring, and for evaluating the effects of restoration measures. In addition, life-history tactics can guide future research into the most fruitful direction.
- Large-scale retention of rainwater reduces the spatial variation in environmental conditions that are relevant to aquatic invertebrates. This promoted the expansion of a few life-history tactics at all water bodies within a compartment, while constraining the other tactics. This results in a decrease of cumulative numbers of species.
- Restoring the regional hydrology to increase groundwater influence is a more promising restoration strategy in bog remnants. Successful conservation of biodiversity in this and other ecosystems will strongly depend on the ability to identify and subsequently strengthen the processes underlying landscape heterogeneity.

Recommendations for future research are:
- To obtain more information on the traits possessed by a species and their functional implication in solving other environmental problems (for instance fish predation)
- To expand the life-history tactics to include other species groups and ecosystems, such as aquatic macroinvertebrates from lotic waters.
- To characterise a pristine bog landscape in terms of life-history tactics. This would enhance our understanding of how different parts of a pristine bog landscape function for aquatic invertebrates and provide additional handholds for restoration.
- To use life-history tactics in macroecology to provide insight into the causal mechanisms underpinning statistical patterns involving large sets of species.

Vragenderveen in autumn (16 September 2004). Photo: Wilco Verberk.

Samenvatting

De invloed van de mens op het landschap is overal aanwezig. Veel soorten staan onder grote druk, doordat aanzienlijke delen van hun oorspronkelijke leefgebied zijn ontgonnen, terwijl de kwaliteit van het resterende leefgebied sterk is aangetast door verzuring, verdroging en vermesting. Bescherming en herstel van de oorspronkelijke biodiversiteit vereist kennis over de koppeling tussen soorten en hun omgeving, oftewel de '*match*' tussen soorten en landschap. Hiermee kunnen de effecten van aantastingen op de biodiversiteit worden begrepen, om vervolgens de meest adequate herstelmogelijkheden te bepalen.

Om deze kennis op te doen is een *case-study* uitgevoerd in het Korenburgerveen, een veengebied in het oosten van Nederland. Van diverse watertypen in dit gebied is de watermacrofauna bestudeerd. **Hoofdstuk 1** geeft een algemene inleiding over de koppeling tussen soorten en hun omgeving en de schaalproblemen die daarbij spelen. Hieruit volgt de centrale vraag van dit proefschrift: "Hoe kunnen we grip krijgen op de grote variatie in relaties tussen soorten en hun omgeving?". Het belangrijkste doel van het proefschrift is dan ook het ontwikkelen, toepassen en evalueren van een methodiek, waarmee relaties tussen soorten en hun omgeving kunnen worden verklaard en samengevoegd tot een beperkt aantal sleutelrelaties.

Eerst is een vergelijkend veldonderzoek uitgevoerd waarbij relaties tussen omgevingscondities, soortensamenstelling en soortenrijkdom van macrofauna zijn beschreven voor het Korenburgerveen en zes andere veengebieden in Nederland. De resultaten van dit veldonderzoek staan beschreven in **hoofdstuk 2**. Dergelijke relaties kunnen complex zijn. Een soort kan bijvoorbeeld voor de overwintering, het vergaren van voedsel en de reproductie gebruik maken van verschillende plekken die in de ruimte gescheiden zijn. Hierdoor kunnen watermacrofaunasoorten gebonden zijn aan een bepaalde vorm van terreinheterogeniteit. De aantastende effecten van verzuring, verdroging en vermesting zorgen echter voor eenzelfde type veranderingen over een groot oppervlak. Daardoor werken deze milieuaantastingen nivellerend op de heterogeniteit van een natuurgebied. Om deze reden is de relatie tussen heterogeniteit en soortenrijkdom verder uitgediept. De soortenrijkdom in veenplassen bleek hoger wanneer het omliggende landschap heterogener was. De soortensamenstelling bleek zowel gecorreleerd met bepaalde omgevingscondities als met de ruimtelijke configuratie. Dergelijke statistische correlaties geven echter nog geen verklaring voor de gevonden relaties tussen soorten en hun omgeving. Hiervoor is het noodzakelijk om causale mechanismen te betrekken in de analyses.

In de loop van de evolutie hebben soorten fysiologische, morfologische en gedragsaanpassingen ontwikkeld, die hen in staat stellen om beter in te spelen op bestaande mogelijkheden of waarmee ze bepaalde problemen in hun leefomgeving kunnen weerstaan of omzeilen. Een verhard exoskelet, diapauze in het eistadium, een korte ontwikkelingsduur en broedzorg zijn slechts enkele voorbeelden van dergelijke aanpassingen. Met dergelijke aanpassingen kunnen de causale mechanismen worden herleid, die de omgevingseisen van een soort verklaren. Om deze soortkenmerken te kunnen gebruiken bij het verklaren van relaties tussen soorten en hun omgeving is onderzocht hoe soortkenmerken met elkaar samenhangen en hoe combinaties van soortkenmerken functioneren. **Hoofdstuk 3** beschrijft het resultaat van deze literatuurstudie. Eén van de problemen bij het groeperen van soorten op basis van hun kenmerken is de veelvoud aan soorten die een nog grotere veelvoud aan kenmerken bezitten in allerlei verschillende combinaties. Het aantal mogelijke combinaties kan echter

worden gereduceerd wanneer men herkent hoe kenmerken met elkaar samenhangen. Zo kunnen kenmerken samenhangen via een *trade-off*, waarbij een grote investering in het ene kenmerk noodzakelijkerwijs gepaard gaat met een kleine(re) investering in een ander kenmerk. Vanuit deze samenhang tussen kenmerken is het mogelijk om het functioneren van combinaties van kenmerken te interpreteren. Afhankelijk van bepaalde combinaties van kenmerken hebben soorten bijvoorbeeld een hogere overlevingskans van eieren, een snellere ontwikkeling of zijn ze beter in staat om risico's te spreiden. Vanuit dit functioneren zijn overlevingsstrategieën afgeleid, die gedefinieerd zijn als "de oplossing voor een bepaald ecologisch probleem, die wordt gegeven door kenmerken die via natuurlijke selectie tot een samenhangende set zijn geëvolueerd". Soorten zijn toegewezen aan overlevingsstrategieën. Soorten van eenzelfde overlevingsstrategie kunnen van elkaar verschillen in de soortkenmerken die ze bezitten, zolang de kenmerken maar eenzelfde type oplossing vormen. Hierdoor zijn soorten van verschillende taxonomische groepen ingedeeld in 13 overlevingsstrategieën.

In **hoofdstuk 4** wordt de indeling in overlevingsstrategieën getoetst met behulp van veldgegevens. De watertypen die in hoofdstuk 2 zijn onderscheiden worden hier beschreven op basis van de relatieve abundanties van individuen van verschillende soorten met dezelfde overlevingsstrategie. Verschillen in de mate, duur en voorspelbaarheid van de geschiktheid van de watertypen konden worden gekoppeld aan verschillen in de dominante strategieën. Bijvoorbeeld, grote matig voedselrijke wateren bieden een stabiele, voorspelbare leefomgeving. Soorten met een lange larvale ontwikkeling en waarbij kortlevende adulten gesynchroniseerd uitsluipen waren hier het meest abundant. Soorten die juist een snelle larvale ontwikkeling hebben, gecombineerd met een over het seizoen gespreide reproductie, waren het meest talrijk in de wateren met fluctuerende en onvoorspelbare condities. Overlevingsstrategieën bieden dus mechanistische verklaringen voor verschillen in het voorkomen en de abundanties van soorten. Hierdoor kan de overweldigende soortenrijkdom worden teruggebracht tot een beperkt aantal overlevingsstrategieën die een duidelijke koppeling met de leefomgeving hebben (voor het toewijzen van soorten aan overlevingsstrategieën blijft determinatie tot op het niveau van de soort echter noodzakelijk). Daarmee bieden overlevingsstrategieën handvatten voor zowel fundamenteel als toegepast ecologisch onderzoek. De toepassing van overlevingsstrategieën op een fundamenteel ecologisch probleem is uitgewerkt in hoofdstuk 5 en in hoofdstuk 6 is de uitwerking voor een toegepast probleem beschreven.

In **hoofdstuk 5** wordt gezocht naar de verklaring voor het wijd verspreide fenomeen dat soorten met een hoge dichtheid ook een brede (geografische) verspreiding hebben. Voor elke overlevingsstrategie werd op basis van de soortkenmerken de dichtheid en verspreiding voorspeld. Deze bleek in goede overeenstemming met de veldgegevens. Zo hadden strategieën met een geclusterde eiafzet of met een snelle vermeerderingssnelheid (bijvoorbeeld via asexuele reproductie) een relatief hoge dichtheid, terwijl strategieën met veel dispersie of een geringe legselgrootte een relatief wijde verspreiding hadden. Daarmee geven overlevingsstrategieën inzicht in de causale mechanismen die ten grondslag liggen aan statistische patronen over grote aantallen soorten.

In **hoofdstuk 6** worden de effecten op de watermacrofauna van grootschalige vernattingsmaatregelen in het Korenburgerveen geëvalueerd met behulp van overlevingsstrategieën. Verdroging werd tegengegaan door het regenwater langer vast te houden via de constructie van dammen in het veen en door ontwatering tegen te gaan via het ondieper maken of dempen van drainerende waterlopen in de omgeving. Het

vasthouden van regenwater leidde tot minder invloed van grondwater, terwijl de verminderde drainage meer invloed van grondwater tot gevolg had. Met de overlevingsstrategieën konden de effecten van deze vernattingsmaatregelen worden gekoppeld aan de veranderingen in de watermacrofauna via mechanistische verklaringen. Het vasthouden van regenwater op grote schaal leidde tot een afname van terreinheterogeniteit en soortenrijkdom. Daarentegen, op plaatsen waar de invloed van grondwater juist (lokaal) was toegenomen, ontwikkelden zich stabielere, minerotrofe overgangssituaties. In intacte veenlandschappen zijn deze stabiele overgangssituaties '*hotspots*' van biodiversiteit. Het vergroten van de invloed van grondwater door herstel van regionale hydrologie is daarom een veelbelovende herstelstrategie. Dit is ook in overeenstemming met de huidige biogeochemische inzichten dat minerotrofe condities een sleutelrol spelen in de primaire en secundaire successie in venen. Deze landschapsvormende processen vormen de motor voor terreinheterogeniteit en hun herstel vergroot daarmee de effectiviteit van herstelplannen voor de fauna.

De betekenis van overlevingsstrategieën voor de synecologie en restoratie ecologie worden besproken in **hoofdstuk 7**. Met de overlevingsstrategieën is het mogelijk om de informatie over aanpassingen van soorten op een geïntegreerde wijze te gebruiken in de synecologie. Doordat overlevingsstrategieën inzicht geven in de causale mechanismen die ten grondslag liggen aan de koppeling tussen soorten en hun omgeving, kunnen ze worden gebruikt om de meest waarschijnlijke verklaring te achterhalen en om voorspellingen te genereren. De toepassingen van overlevingsstrategieën in hoofdstuk 5 en 6 zijn daar voorbeelden van. Overlevingsstrategieën bieden de mogelijkheid om informatie te aggregeren over vele soorten van verschillende taxonomische eenheden, met behoud van de informatie over de causale mechanismen. Hierdoor slaan ze een brug tussen de aanpak vanuit soorten en die vanuit gemeenschappen. In de laatstgenoemde benadering wordt informatie over veel verschillende soorten geaggregeerd, bijvoorbeeld in indicatoren voor biodiversiteit, waarbij de causale mechanismen uit beeld verdwijnen. Met de aanpak vanuit afzonderlijke soorten wordt wel sterk de nadruk gelegd op de causale mechanismen voor één of enkele soorten, maar hier is juist de aggregatie lastig, omdat onduidelijk is hoe belangrijk de gevonden mechanismen zijn ten opzichte van andere soorten. Door het verenigen van deze sterke punten van causaliteit en aggregatie kunnen overlevingsstrategieën van betekenis zijn voor het vakgebied van macroecologie, waarbij gezocht wordt naar statistische patronen over grote aantallen soorten.

Terreinheterogeniteit speelt een belangrijke rol in het behouden van biodiversiteit, gezien de nauwe relatie tussen beiden. Terreinheterogeniteit ontstaat door het samenspel van abiotische condities en talloze organismen van vele soorten. Dit maakt een direct herstel van terreinheterogeniteit lastig. De beste optie is daarom om de processen te herstellen die indirect leiden tot terreinheterogeniteit. Dit kan neerkomen op het creëren van de juiste abiotische randvoorwaarden, het bevorderen van bepaalde soorten of een combinatie van beide. Overlevingsstrategieën geven inzicht in het functioneren van een ecosysteem en daarmee in het relatieve belang van abiotische randvoorwaarden en interacties tussen soorten. Het succesvol behouden van soorten zal in belangrijke mate afhankelijk zijn van het identificeren en vervolgens het herstellen van de processen die ten grondslag liggen aan de terreinheterogeniteit.

De belangrijkste conclusies die voortkomen uit het onderzoek dat in dit proefschrift is beschreven:
- Heterogene veenlandschappen hebben een hogere soortenrijkdom dan meer homogene veenlandschappen. De terreinheterogeniteit speelt hierbij een belangrijke rol, onder andere doordat soorten worden gefaciliteerd die afhankelijk zijn van een combinatie van habitattypen, die gebonden zijn aan overgangsmilieu's of doordat populaties zich beter kunnen handhaven.
- Soortkenmerken hangen nauw met elkaar samen. Met een functionele interpretatie van combinaties van kenmerken is het mogelijk om een coherente synthese naar overlevingsstrategieën (life-history tactics) te maken vanuit de biologische verschillen tussen de vele soorten watermacrofauna.
- Overlevingsstrategieën zijn gestoeld op de causale mechanismen die ten grondslag liggen aan de koppeling tussen soorten en hun omgeving, ofwel de '*match*' tussen soorten en landschap. Door de meest waarschijnlijke verklaring te achterhalen en voorspellingen te genereren, kunnen ze toekomstig onderzoek aansturen. Daarbij biedt deze methodiek handvatten voor biologische monitoring en ecologische beoordelingen, waaronder evaluaties van de effecten van herstelmaatregelen.
- Grootschalig vernatten door regenwater vast te houden werkt nivellerend op de omgevingscondities die relevant zijn voor watermacrofauna. Dit bevordert overal een klein aantal soorten met dezelfde overlevingsstrategie, ten koste van de andere soorten die van plek tot plek kunnen verschillen. Dit resulteert in een afname van de soortenrijkdom.
- Herstel van de regionale hydrologie om zo de grondwaterinvloed te versterken is een veelbelovende herstelstrategie in veenrestanten. Het succes om soorten te behouden in veenrestanten en andere ecosystemen zal in belangrijke mate afhankelijk zijn van het identificeren en vervolgens het herstellen van de processen die ten grondslag liggen aan de terreinheterogeniteit.

Aanbevelingen voor toekomstig onderzoek aan overlevingsstrategieën zijn:
- Meer informatie achterhalen van kenmerken van soorten en hun functionele betekenis om bepaalde problemen in hun leefomgeving het hoofd te bieden (bijvoorbeeld vispredatie).
- Overlevingsstrategieën achterhalen voor meer soorten in andere systemen (bijvoorbeeld de watermacrofauna in stromende wateren).
- Een intact veenlandschap karakteriseren in termen van overlevingsstrategieën. Dit geeft extra inzicht hoe in een meer intact veenlandschap de verschillende landschapsonderdelen functioneren. Dit biedt extra handvatten voor herstel van veenrestanten.
- Overlevingsstrategieën inzetten om grip te krijgen op de causale mechanismen die ten grondslag liggen aan algemene wetmatigheden over grote aantallen soorten.

A female of the northern emerald (Somatochlora arctica) that has just emerged from its larval skin. Photo: Wilco Verberk.

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The author and his daughter Saar, exploring. Photo: Hanny de Jonge-Wubben.

Curriculum vitae

Wilhelmus Cornelis Egbertus Petrus (Wilco) Verberk werd geboren op 30 juni 1976 te Ofloo. Na het behalen van het VWO diploma aan het Elzendaal College in Boxmeer begon hij in 1994 met zijn studie Biologie aan de Katholieke Universiteit Nijmegen (thans Radboud Universiteit Nijmegen). De keuze voor een onderzoeksstage bij de afdeling Cellulaire Dierfysiologie werd ingegeven door zijn interesse naar het bewustzijn en geheugen van het menselijke brein. Zijn tweede onderzoeksstage naar tropische vissen op de koraalriffen en zeegrasvelden van Curaçao stond in het teken van de problemen, improvisaties en vooral de fascinatie die gepaard gaan met ecologisch veldonderzoek. Na zijn terugkomst heeft hij bij het Instituut voor Bos- en Natuuronderzoek (thans Alterra) onderzoek verricht naar herstelde bronnen in Overijssel waar hij de herkolonisatie door watermacrofauna volgde. Ondertussen verdiepte hij zich verder in het functioneren en de structuur van andere ecosystemen in Nederland. Zo heeft hij in zijn vrije tijd menige beek in Limburg met steeknetten bemonsterd op vissen. Na zijn afstuderen in 2000 is hij bij de stichting Bargerveen gestart met het onderzoek naar de betekenis van terreinheterogeniteit voor de faunadiversiteit. Tijdens deze periode was hij gastmedewerker bij de afdeling Dierecologie en -ecofysiologie van de Radboud Universiteit Nijmegen. Het onderzoek werd gefinancierd vanuit het Overlevingsplan Bos + Natuur (OB+N), een onderzoeksprogramma van het ministerie van Landbouw, Natuurbeheer en Visserij (thans Landbouw, Natuurbeheer en Voedselkwaliteit). Tijdens dit onderzoek ontwikkelde hij een methode om vanuit soorteigenschappen verschillen in de soortensamenstelling van watermacrofauna tussen wateren te verklaren. De aanleiding, ontwikkeling en toepassing van deze methode staan beschreven in dit proefschrift. Naast zijn onderzoeksactiviteiten verzorgde hij diverse hoorcolleges voor universitaire studenten, begeleidde hij een groot aantal studenten, organiseerde hij verschillende veldexcursies in binnen- en buitenland en hield hij voordrachten op nationale bijeenkomsten en internationale congressen. Bovendien was hij intensief betrokken bij diverse andere onderzoeksprojecten in het kader van natuurbeheer en -herstel. Op het ogenblik is hij lid van verschillende nationale deskundigenteams in het kader van Ontwikkeling + Beheer Natuurkwaliteit (O+BN), waar hij zijn ideeën en kennis kan inzetten om problemen op te lossen en mogelijkheden te benutten in het Nederlandse natuurbeheer. In de toekomst wil hij het effect van soorten op elkaar en hun omgeving onderzoeken met dezelfde aanpak vanuit soorteigenschappen. Niet-werkgerelateerde mijlpalen zijn het huwelijk met Lies Janne de Jonge (2001), de geboorte van Saar Hanna Verberk (2005) en de geboorte van Toon Cornelis Verberk (2007).

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A chironomid larvae. These larvae were collected in the Korenburgerveen, reared to adulthood and subsequently identified as Lasiodiamesa gracilis, which turned out to be a new species for the Netherlands. Photo: René Krekels.

Appendix

Appendix 1 List of taxa captured and their life history tactic. For each taxa the number of occupied water bodies is listed, both before and after measures were taken.

Scientific name	Systematic group	Tactic	# water bodies Before	After
Dugesia polychroa (Schmidt, 1861)	Tricladida	S4	2	0
Planaria torva (Müller, 1773)	Tricladida	R2	4	5
Polycelis tenuis Ijima, 1884	Tricladida	S4	12	19
Dendrocoelum lacteum (Müller, 1774)	Tricladida	R2	8	10
Glossiphonia complanata (Linnaeus, 1758)	Hirudinea	S4	5	5
Glossiphonia heteroclita Linnaeus, 1761	Hirudinea	R3	1	0
Helobdella stagnalis (Linnaeus, 1758)	Hirudinea	R3	4	0
Haemopis sanguisuga Linnaeus, 1758	Hirudinea	S4	2	0
Erpobdella octoculata (Linnaeus, 1758)	Hirudinea	R2	2	2
Erpobdella testacea (Savigny, 1822)	Hirudinea	R2	10	9
Nais variabilis Piguet, 1906	Oligochaeta	R4	13	17
Slavina appendiculata (d'Udekem, 1855)	Oligochaeta	R4	9	6
Vejdovskiella comata (Vejdovsky, 1883)	Oligochaeta	S4	1	1
Haemonais waldvogeli Bretscher, 1900	Oligochaeta	R4	1	0
Dendrobaena octaedra (Savigny, 1826)	Oligochaeta	T2	2	0
Fridericia sp.	Oligochaeta	S4	1	0
Dero digitata (Müller, 1773)	Oligochaeta	R4	13	8
Dero dorsalis Ferronière, 1889	Oligochaeta	R4	10	10
Dero obtusa d'Udekem, 1855	Oligochaeta	R4	5	1
Pristina aequiseta Bourne, 1891	Oligochaeta	S4	1	1
Tubifex tubifex (Müller, 1774)	Oligochaeta	R4	2	4
Limnodrilus claparedeanus Ratzel, 1868	Oligochaeta	S4	1	1
Limnodrilus hoffmeisteri Claparède, 1862	Oligochaeta	R4	7	2
Potamothrix hammoniensis (Michaelsen, 1901)	Oligochaeta	S4	1	0
Potamothrix heuscheri (Bretscher, 1900)	Oligochaeta	S4	1	1
Aulodrilus pluriseta (Piguet, 1906)	Oligochaeta	T2	2	1
Mesenchytraeus sp.	Oligochaeta	S4	1	1
Cognettia glandulosa (Michaelsen, 1888)	Oligochaeta	T2	13	24
Cognettia sphagnetorum (Vejdovský, 1878)	Oligochaeta	T2	4	0
Stylodrilus sp.	Oligochaeta	S4	3	0
Lumbriculus variegatus (Müller, 1774)	Oligochaeta	T2	27	29
Rhynchelmis limosella Hoffmeister, 1843	Oligochaeta	S4	4	0
Eiseniella tetraedra (Savigny, 1826)	Oligochaeta	T2	1	2
Asellus aquaticus (Linnaeus, 1758)	Crustacea	R3	29	30
Argyroneta aquatica (Clerck, 1757)	Arachnida	T1	22	36
Cymatia bonsdorffi (Sahlberg, 1819)	Hemiptera	T1	1	0
Cymatia coleoptrata (Fabricius, 1777)	Hemiptera	R1	2	1
Corixa dentipes Thomson, 1869	Hemiptera	D1	0	1
Corixa punctata (Illiger, 1807)	Hemiptera	D1	2	3
Hesperocorixa castanea (Thomson, 1869)	Hemiptera	T1	4	6
Hesperocorixa linnaei (Fieber, 1848)	Hemiptera	D1	8	3
Hesperocorixa sahlbergi (Fieber, 1848)	Hemiptera	D1	26	28
Sigara distincta (Fieber, 1848)	Hemiptera	D3	0	0
Sigara semistriata (Fieber, 1848)	Hemiptera	T1	0	2
Sigara striata (Linnaeus, 1758)	Hemiptera	D3	1	0
Ilyocoris cimicoides (Linnaeus, 1758)	Hemiptera	T1	8	8
Nepa cinerea Linnaeus, 1758	Hemiptera	T1	0	2
Ranatra linearis (Linnaeus, 1758)	Hemiptera	R1	0	2
Plea minutissima Leach, 1817	Hemiptera	T1	11	9
Notonecta glauca Linnaeus, 1758	Hemiptera	D1	6	14
Notonecta obliqua Thunberg, 1787	Hemiptera	D1	3	1
Notonecta viridis Delcourt, 1909	Hemiptera	D1	1	0
Hydrometra gracilenta Horváth, 1899	Hemiptera	R1	0	3
Hydrometra stagnorum (Linnaeus, 1758)	Hemiptera	R1	1	9
Hebrus pusillus (Fallén, 1807)	Hemiptera	D3	6	1
Hebrus ruficeps Thomson, 1871	Hemiptera	R1	8	14

Appendix 1 Continued

Scientific name	Systematic group	Tactic	# water bodies Before	After
Microvelia reticulata (Burmeister, 1835)	Hemiptera	R1	13	20
Microvelia buenoi Drake, 1920	Hemiptera	R1	10	22
Gerris gibbifer Schummel, 1832	Hemiptera	D3	0	0
Gerris lacustris (Linnaeus, 1758)	Hemiptera	R1	1	2
Gerris lateralis Schummel, 1832	Hemiptera	R1	1	1
Gerris odontogaster Zetterstedt, 1828	Hemiptera	D3	3	2
Lestes viridis (Van der Linden, 1825)	Odonata	S2	2	2
Ischnura elegans (Van der Linden, 1820)	Odonata	D2	1	2
Pyrrhosoma nymphula (Sulzer, 1776)	Odonata	T1	20	30
Enallagma cyathigerum (Charpentier, 1840)	Odonata	D2	0	1
Coenagrion hastulatum (Charpentier, 1825)	Odonata	T1	6	3
Coenagrion puella (Linnaeus, 1758) / *C. pulchellum* (Van der Linden, 1825)	Odonata	S1	13	16
Ceriagrion tenellum (de Villers, 1789)	Odonata	T1	5	11
Aeshna cyanea (Müller, 1764)	Odonata	S1	4	2
Aeshna juncea (Linnaeus, 1758)	Odonata	S1	0	1
Brachytron pratense (Müller, 1764)	Odonata	T1	0	1
Cordulia aenea (Linnaeus, 1758)	Odonata	T1	2	3
Libellula depressa Linnaeus, 1758	Odonata	D2	0	1
Libellula quadrimaculata Linnaeus, 1758	Odonata	D2	5	12
Sympetrum danae (Sulzer, 1776)	Odonata	S2	1	0
Sympetrum sanguineum (Müller, 1764)	Odonata	S2	1	0
Sympetrum striolatum (Charpentier, 1840)	Odonata	D2	1	0
Sympetrum vulgatum (Linnaeus, 1758)	Odonata	S2	2	3
Leucorrhinia dubia (Van der Linden, 1825)	Odonata	T1	5	1
Leucorrhinia rubicunda (Linnaeus, 1758)	Odonata	T1	11	12
Nemoura cinerea (Retzius, 1783)	Plecoptera	T1	3	8
Beraeodes minutus (Linnaeus, 1761)	Trichoptera	S1	1	0
Athripsodes aterrimus (Stephens, 1836)	Trichoptera	D1	0	1
Triaenodes bicolor (Curtis, 1834)	Trichoptera	D1	5	6
Glyphotaelius pellucidus (Retzius, 1783)	Trichoptera	S2	7	1
Limnephilus decipiens (Kolenati, 1848)	Trichoptera	S2	0	1
Limnephilus elegans Curtis, 1834	Trichoptera	S2	3	4
Limnephilus flavicornis (Fabricius, 1787)	Trichoptera	S2	6	6
Limnephilus lunatus Curtis, 1834	Trichoptera	S2	4	2
Limnephilus nigriceps (Zetterstedt, 1840)	Trichoptera	S2	1	1
Limnephilus stigma Curtis, 1834	Trichoptera	S2	2	3
Limnephilus subcentralis Brauer, 1857	Trichoptera	S2	0	1
Anabolia brevipennis (Curtis, 1834)	Trichoptera	D1	0	3
Agrypnia varia (Fabricius, 1793)	Trichoptera	T1	1	1
Hagenella clathrata (Kolenati, 1848)	Trichoptera	S2	4	3
Oligotricha striata (Linnaeus, 1758)	Trichoptera	T1	15	24
Trichostegia minor (Curtis, 1834)	Trichoptera	S1	12	16
Holocentropus dubius (Rambur, 1842)	Trichoptera	T1	4	4
Holocentropus picicornis (Stephens, 1836)	Trichoptera	T1	1	0
Holocentropus stagnalis (Albarda, 1874)	Trichoptera	T1	9	7
Sialis sp.	Megaloptera	T1	2	2
Cloeon dipterum (Linnaeus, 1761)	Ephemeroptera	D2	15	18
Hygrobia hermanni (Fabricius, 1775)	Coleoptera	T1	1	0
Peltodytes caesus (Duftschmid, 1805)	Coleoptera	T1	4	2
Haliplus fluviatilis Aubé, 1836	Coleoptera	R1	1	0
Haliplus fulvicollis Erichson, 1837	Coleoptera	T1	4	6
Haliplus heydeni Wehncke, 1875	Coleoptera	R1	4	2
Haliplus immaculatus Gerhardt, 1877	Coleoptera	R1	2	0
Haliplus lineolatus Mannerheim, 1844	Coleoptera	R1	0	1
Haliplus ruficollis (De Geer, 1774)	Coleoptera	R1	10	7
Haliplus lineolatus Mannerheim 1844	Coleoptera	R1	0	1
Noterus clavicornis (De Geer, 1774)	Coleoptera	T1	2	1

Appendix 1 Continued

Scientific name	Systematic group	Tactic	# water bodies Before	After
Noterus crassicornis (Müller, 1776)	Coleoptera	T2	25	33
Laccophilus minutus (Linnaeus, 1758)	Coleoptera	D1	2	2
Hyphydrus ovatus (Linnaeus, 1761)	Coleoptera	T1	4	1
Hydroglyphus pusillus (Fabricius, 1781)	Coleoptera	D1	1	2
Bidessus grossepunctatus Vorbringer, 1907	Coleoptera	R1	0	2
Bidessus unistriatus (Schrank, 1781)	Coleoptera	R1	0	2
Hygrotus impressopunctatus (Schaller, 1783)	Coleoptera	D1	2	4
Hygrotus decoratus (Gyllenhal, 1810)	Coleoptera	T1	16	22
Hygrotus inaequalis (Fabricius, 1777)	Coleoptera	T1	19	21
Hydroporus angustatus Sturm, 1835	Coleoptera	D1	8	8
Hydroporus erythrocephalus (Linnaeus, 1758)	Coleoptera	S3	22	26
Hydroporus gyllenhalii Schidte, 1841	Coleoptera	R1	15	12
Hydroporus incognitus Sharp, 1869	Coleoptera	D1	0	3
Hydroporus melanarius Sturm, 1835	Coleoptera	D1	2	0
Hydroporus neglectus Schaum, 1845	Coleoptera	R1	6	8
Hydroporus obscurus Sturm, 1835	Coleoptera	T1	17	20
Hydroporus palustris (Linnaeus, 1761)	Coleoptera	R1	7	6
Hydroporus planus (Fabricius, 1781)	Coleoptera	D1	4	1
Hydroporus scalesianus Stephens, 1828	Coleoptera	S3	6	8
Hydroporus striola (Gyllenhal, 1826)	Coleoptera	S3	1	1
Hydroporus tristis (Paykull, 1798)	Coleoptera	R1	20	19
Hydroporus umbrosus (Gyllenhal, 1808)	Coleoptera	S3	28	32
Hydroporus morio Aubé, 1838	Coleoptera	S3	0	0
Porhydrus lineatus (Fabricius, 1775)	Coleoptera	D1	5	3
Graptodytes granularis (Linnaeus, 1767)	Coleoptera	R1	2	2
Graptodytes pictus (Fabricius, 1787)	Coleoptera	R1	4	1
Laccornis oblongus (Stephens, 1835)	Coleoptera	S3	1	2
Suphrodytes dorsalis (Fabricius, 1787)	Coleoptera	D1	5	9
Copelatus haemorrhoidalis (Fabricius, 1787)	Coleoptera	D1	3	11
Agabus affinis (Paykull, 1798)	Coleoptera	R1	5	5
Agabus bipustulatus (Linnaeus, 1767)	Coleoptera	D1	23	15
Agabus congener (Thunberg, 1794)	Coleoptera	S2	4	2
Agabus striolatus (Gyllenhal, 1808)	Coleoptera	S3	2	0
Agabus sturmii (Gyllenhal, 1808)	Coleoptera	D1	13	14
Agabus uliginosus (Linnaeus, 1761)	Coleoptera	S3	1	1
Agabus undulatus (Schrank, 1776)	Coleoptera	S3	3	4
Agabus unguicularis (Thomson, 1867)	Coleoptera	S3	1	4
Ilybius aenescens Thomson, 1870	Coleoptera	S2	19	16
Ilybius ater (De Geer, 1774)	Coleoptera	S2	7	20
Ilybius fenestratus (Fabricius, 1781)	Coleoptera	S2	2	0
Ilybius fuliginosus (Fabricius, 1792)	Coleoptera	S2	0	1
Ilybius guttiger (Gyllenhal, 1808)	Coleoptera	S2	15	16
Ilybius quadriguttatus (Lacordaire, 1835)	Coleoptera	S2	3	10
Ilybius subaeneus Erichson, 1837	Coleoptera	S2	1	0
Rhantus exsoletus (Forster, 1771)	Coleoptera	D1	0	1
Rhantus suturalis (MacLeay, 1825)	Coleoptera	D1	1	0
Rhantus suturellus (Harris, 1828)	Coleoptera	S3	1	0
Rhantus grapii (Gyllenhal, 1808)	Coleoptera	D1	5	11
Colymbetes paykulli Erichson, 1837	Coleoptera	S3	3	5
Hydaticus seminiger (De Geer, 1774)	Coleoptera	D1	4	12
Acilius canaliculatus (Nicolai, 1822)	Coleoptera	D1	16	24
Acilius sulcatus (Linnaeus, 1758)	Coleoptera	D1	2	4
Dytiscus circumcinctus Ahrens, 1811	Coleoptera	S3	0	2
Dytiscus dimidiatus Bergsträsser, 1778	Coleoptera	S3	1	6
Dytiscus marginalis Linnaeus, 1758	Coleoptera	D1	7	6
Hydraena britteni Joy, 1907	Coleoptera	R1	1	0
Hydraena palustris Erichson, 1837	Coleoptera	R1	4	6
Hydraena testacea Curtis, 1830	Coleoptera	R1	1	3

Appendix 1 Continued

Scientific name	Systematic group	Tactic	# water bodies Before	After
Limnebius aluta Bedel, 1881	Coleoptera	R1	2	4
Helophorus aquaticus (Linnaeus, 1758)	Coleoptera	D1	1	1
Helophorus brevipalpis Bedel, 1881	Coleoptera	D1	6	0
Helophorus nanus Sturm, 1836	Coleoptera	D1	1	0
Helophorus obscurus Mulsant, 1844	Coleoptera	T1	0	1
Helophorus aequalis Thomson, 1868	Coleoptera	D1	1	1
Hydrochus brevis (Herbst, 1793)	Coleoptera	R1	3	3
Hydrochus carinatus Germar, 1824	Coleoptera	R1	11	17
Hydrochus megaphallus van Berge Henegouwen, 1988	Coleoptera	R1	2	0
Coelostoma orbiculare (Fabricius, 1775)	Coleoptera	T1	0	2
Cercyon convexiusculus Stephens, 1829	Coleoptera	D1	2	2
Cercyon sternalis (Sharp, 1918)	Coleoptera	D1	0	2
Hydrobius fuscipes (Linnaeus, 1758)	Coleoptera	R1	12	12
Anacaena globulus (Paykull, 1798)	Coleoptera	T1	8	6
Anacaena limbata (Fabricius, 1792)	Coleoptera	T1	8	8
Anacaena lutescens (Stephens, 1829)	Coleoptera	D1	25	19
Laccobius bipunctatus (Fabricius, 1775)	Coleoptera	T1	0	1
Laccobius sinuatus Motschulsky, 1849	Coleoptera	T1	1	0
Helochares lividus (Forster, 1771)	Coleoptera	S3	2	0
Helochares punctatus Sharp, 1869	Coleoptera	S3	11	15
Enochrus affinis (Thunberg, 1794)	Coleoptera	S3	11	18
Enochrus coarctatus (Gredler, 1863)	Coleoptera	S3	6	24
Enochrus melanocephalus (Olivier, 1792)	Coleoptera	S3	2	0
Enochrus ochropterus (Marsham, 1802)	Coleoptera	S3	10	21
Enochrus testaceus (Fabricius, 1801)	Coleoptera	S3	1	1
Enochrus fuscipennis (Thomson, 1884)	Coleoptera	S3	1	0
Cymbiodyta marginella (Fabricius, 1792)	Coleoptera	S3	6	14
Hydrophilus piceus (Linnaeus, 1758)	Coleoptera	S3	1	1
Berosus luridus (Linnaeus, 1761)	Coleoptera	T1	0	1
Scirtes sp.	Coleoptera	S1	3	5
Cyphon sp.	Coleoptera	T1	20	22
Microcara testacea (Linnaeus, 1767)	Coleoptera	S1	12	9
Phalacrocera replicata (Linnaeus, 1758)	Diptera	T1	10	17
Mochlonyx martinii Edwards, 1930	Diptera	S2	8	8
Mochlonyx velutinus (Ruthe, 1831)	Diptera	S2	4	3
Chaoborus crystallinus (de Geer, 1776)	Diptera	S1	23	17
Chaoborus flavicans (Meigen, 1830)	Diptera	S1	10	3
Chaoborus obscuripes (van der Wulp, 1859)	Diptera	S2	8	3
Chaoborus pallidus (Fabricius, 1794)	Diptera	T1	21	24
Dixella aestivalis (Meigen, 1818)	Diptera	D1	1	4
Dixella amphibia (de Geer, 1776)	Diptera	D3	17	20
Dixella autumnalis (Meigen, 1838)	Diptera	D1	1	3
Dixella serotina (Meigen, 1818)	Diptera	D3	0	2
Anopheles claviger (Meigen, 1804)	Diptera	D3	1	0
Anopheles gr. *maculipennis* Meigen, 1818	Diptera	D1	0	1
Mansonia richiardii (Ficalbi, 1889)	Diptera	S1	5	7
Aedes cinereus Meigen, 1818	Diptera	S2	2	1
Aedes geniculatus (Olivier, 1791)	Diptera	R1	2	0
Aedes punctor (Kirby in Richardson, 1837)	Diptera	S2	3	4
Aedes annulipes (Meigen, 1830) / *A. cantans* (Meigen, 1818)	Diptera	S2	2	12
Culiseta alaskaensis (Ludlow, 1906)	Diptera	D3	2	1
Culiseta annulata (Schrank, 1776)	Diptera	D3	1	2
Culiseta subochrea (Edwards, 1921)	Diptera	D3	0	0
Culiseta morsitans (Theobald, 1901)	Diptera	R1	11	17
Culex territans Walker, 1856	Diptera	D3	0	2
Lasiodiamesa gracilis Kieffer, 1924	Diptera	S1	6	2
Ablabesmyia phatta (Egger, 1863)	Diptera	D1	7	2
Ablabesmyia longistyla Fittkau, 1962 / *A .monilis* (Linnaeus, 1758)	Diptera	D1	6	2

Appendix 1 Continued

Scientific name	Systematic group	Tactic	# water bodies Before	# water bodies After
Guttipelopia guttipennis (van der Wulp, 1861)	Diptera	S1	4	0
Macropelopia sp.	Diptera	T1	0	2
Monopelopia tenuicalcar (Kieffer, 1918)	Diptera	S1	25	24
Natarsia punctata (Meigen, 1804)	Diptera	T1	13	13
Schineriella schineri (Strobl, 1880)	Diptera	S1	0	1
Paramerina cingulata (Walker, 1856)	Diptera	D1	3	4
Procladius choreus (Meigen, 1804)	Diptera	S1	14	22
Psectrotanypus varius (Fabricius, 1787)	Diptera	D1	6	1
Telmatopelopia nemorum (Goetghebuer, 1921)	Diptera	S1	19	22
Xenopelopia sp.	Diptera	D1	27	20
Zavrelimyia sp.	Diptera	S1	4	2
Acricotopus lucens (Zetterstedt, 1850)	Diptera	D1	6	6
Chaetocladius piger agg.	Diptera	S1	0	2
Chaetocladius sp. *herkenbosch*	Diptera	S1	3	9
Corynoneura scutellata agg.	Diptera	D3	5	5
Cricotopus brevipalpis Kieffer, 1909	Diptera	D3	1	0
Cricotopus cylindraceus (Kieffer in Kieffer & Thienemann, 1908) / *C. festivellus* (Kieffer, 1906)	Diptera	D1	0	1
Cricotopus trifasciatus agg.	Diptera	D1	1	0
Cricotopus sylvestris agg.	Diptera	D1	0	2
Limnophyes sp.	Diptera	D3	10	24
Orthocladius holsatus Goetghebuer, 1937	Diptera	D1	1	1
Paralimnophyes hydrophilus (Goetghebuer, 1921)	Diptera	D3	7	5
Psectrocladius obvius (Walker, 1856)	Diptera	S1	0	1
Psectrocladius platypus (Edwards, 1929)	Diptera	D1	16	21
Psectrocladius gr. *psilopterus*	Diptera	D1	4	5
Psectrocladius gr. *sordidellus/limbatellus*	Diptera	D1	1	3
Pseudosmittia sp.	Diptera	D3	1	1
Chironomus sp.	Diptera	T1	31	39
Cladopelma gr. *lateralis*	Diptera	T1	2	3
Dicrotendipes nervosus (Staeger, 1839)	Diptera	T1	0	1
Dicrotendipes notatus (Meigen, 1818)	Diptera	T1	1	0
Dicrotendipes gr. *lobiger*	Diptera	T1	3	3
Dicrotendipes gr. *tritomus*	Diptera	T1	2	1
Endochironomus albipennis (Meigen, 1830)	Diptera	S1	1	0
Endochironomus tendens (Fabricius, 1775)	Diptera	T1	4	4
Endochironomus gr. *dispar*	Diptera	T1	13	20
Glyptotendipes foliicola Kieffer, 1918	Diptera	T1	3	0
Glyptotendipes caulicola (Kieffer, 1913)	Diptera	T1	0	4
Glyptotendipes paripes (Edwards, 1929)	Diptera	T1	1	3
Glyptotendipes gripekoveni (Kieffer, 1913)	Diptera	T1	3	2
Parachironomus arcuatus (Goetghebuer, 1919)	Diptera	D1	1	0
Paratendipes gr. *nudisquama*	Diptera	T1	3	3
Polypedilum gr. *sordens*	Diptera	T1	3	4
Polypedilum uncinatum agg.	Diptera	T1	28	25
Zavreliella marmorata (van der Wulp, 1858)	Diptera	D1	1	2
Cladotanytarsus sp.	Diptera	T1	2	1
Micropsectra lindrothi Goetghebuer, 1931	Diptera	T1	0	1
Paratanytarsus sp.	Diptera	S1	3	11
Tanytarsus sp.	Diptera	T1	6	5
Zavrelia sp.	Diptera	S1	4	5
Ceratopogonidae	Diptera	T1	43	43

Het Nederlands Centrum voor Natuuronderzoek (NCN) ontwikkelt, bundelt en verspreidt kennis op het gebied van herstel en behoud van biodiversiteit. De volgende organisaties participeren in het NCN:
- Faculteit der Natuurwetenschappen, Wiskunde en Informatica van de Radboud Universiteit (RU) Nijmegen
- De afdelingen Aquatische Ecologie & Milieubiologie, Dierecologie en -ecofysiologie en Milieukunde van de RU Nijmegen
- Stichting Bargerveen
- Vereniging SOVON Vogelonderzoek Nederland
- Stichting Reptielen, Amfibieën en Vissen Onderzoek Nederland (RAVON)
- Vereniging Onderzoek Flora en Fauna (VOFF)

De combinatie van organisaties garandeert een goede koppeling tussen het meer correlatieve verspreidingsonderzoek, het wetenschappelijk onderzoek naar causale factoren (met verspreidingsgegevens en lab-, veld- en beheersexperimenten) en de vertaling naar modellen.

Stichting Bargerveen heeft als doel het ontwikkelen van kennis voor herstel en behoud van faunagemeenschappen en het (inter)nationaal verspreiden van deze kennis. Een tweede doel is het bijdragen aan de opleiding van studenten en junior onderzoekers. Zo vormen de onderzoeksprojecten tevens opleidingstrajecten voor junioronderzoekers, uitmondend in promoties.

Onderzoek richt zich onder meer op de effecten van zogenaamde VER-factoren, zoals verzuring, vermesting en verdroging, alsmede de effectiviteit van beheersmaatregelen om deze aantastingen tegen te gaan. Het onderzoek wordt uitgevoerd in binnen- en buitenland in een scala van landschappen, waaronder stuifzanden, kustduinen, kalkgraslanden, laagveenwateren, hoogvenen, heide en vennen.

Stichting Bargerveen is gehuisvest binnen de Radboud Universiteit Nijmegen en werkt nauw samen met de afdelingen dierecologie en -ecofysiologie, milieukunde, aquatische ecologie & milieubiologie van de RU Nijmegen.