

Applying life-history strategies for freshwater macroinvertebrates to lentic waters

WILCO C. E. P. VERBERK^{*,†}, HENK SIEPEL^{*,‡} AND HANS ESSELINK^{*,†}

^{*}*Department of Animal Ecology and Ecophysiology, Institute for Wetland and Water Research, Radboud University Nijmegen, Nijmegen, The Netherlands*

[†]*Bargerveen Foundation, Radboud University Nijmegen, Nijmegen, The Netherlands*

[‡]*Alterra Green World Research, Centre for Ecosystem Studies, Wageningen, The Netherlands*

SUMMARY

1. Effective environmental 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 strategies, based on the interrelations between species traits and their functional implications.
2. This study tests the hypothesis that life-history strategies represent different solutions to particular ecological problems, thus connecting species and their environment through species traits. Data on aquatic macroinvertebrates in a variety of waterbodies were analysed in terms of life-history strategies. These waterbodies differed in environmental conditions and macroinvertebrate assemblages. Solutions to the ecological problems present in each type of water body were expected to be reflected in the abundance of (species exhibiting) different life-history strategies.
3. Results show clear differences in strategy composition between the different water types, which could be related to the prevailing environmental conditions through mechanistic explanations. For example, species with a long period of juvenile development and a synchronized emergence of short-lived adults were most dominant in large mesotrophic waterbodies with stable and predictable environmental conditions. In contrast, species that have a rapid development and spread successive reproduction attempts over a longer time period were most abundant in waterbodies with fluctuating and less predictable environmental conditions.
4. Differences in strategy composition provide insight into the prevailing environmental conditions related to temporal predictability, and habitat favourability, from the perspective of the species themselves. By reducing diverse species assemblages to a small number of strategies, representing easily interpretable relationships, this approach may be useful in environmental quality assessment programmes, including those required by the European Water Framework Directive. Based on mechanistic explanations, life-history strategies may generate testable predictions and guide future research. Further research may focus on expanding life-history strategies to include other species groups and ecosystems.

Keywords: biomonitoring, causal mechanisms, indicator species, species traits, water framework directive

Correspondence: Wilco C. E. P. Verberk, Department of Animal Ecology and Ecophysiology, Institute for Wetland and Water Research, Radboud University Nijmegen, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands. E-mail: w.verberk@science.ru.nl

Introduction

The use of macroinvertebrates in ecological assessment and biomonitoring has a long tradition (Rosenberg & Resh, 1993; Bonada *et al.*, 2006). Water managers have a wide variety of tools at their disposal (Verdonschot, 2000). These tools range from simple indices, such as diversity indices, EPT-taxon richness or the *Gammarus* : *Asellus* ratio, to more advanced and complex methods such as multimetrics or multivariate analytical techniques (e.g. Whitehurst, 1991; Wallace, Grubaugh & Whiles, 1996; Thorne & Williams, 1997; Chessman, 1999). The complex methods used to analyse species-environment relationships, may generate different results, with little indication as to which result best reflects reality (Nijboer, 2006). Thus, all these methods or analytical tools can generate testable predictions (Verdonschot, 2000), but do not give scientific understanding, which ultimately comes from mechanistic explanations (Weiner, 1995). A framework of causal mechanisms is required for effective management (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).

Because species traits determine the ability of a species to deal with environmental problems and opportunities, they can potentially be used to explain occurrence under particular environmental conditions (e.g. Keddy, 1992; McGill *et al.*, 2006). Many studies have successfully related species traits to differences in species occurrence between locations or periods (Statzner, Resh & Dolédec, 1994; Bremner, Rogers & Frid, 2006; Van Kleef *et al.*, 2006). Consequently, trait-based analyses are considered to be a better candidate for biomonitoring than taxon-based analyses (Statzner *et al.*, 2001; Bonada *et al.*, 2006; Mouillot *et al.*, 2006). Trait-based analyses range from clustering species with similar suites of traits (Usseglio-Polatera *et al.*, 2000; Ilg & Castella, 2006), to analysing the co-structure between patterns in species traits and patterns in habitat use with multivariate analytical techniques (Gayraud *et al.*, 2003; Finn & Poff, 2005). In such studies, associations between the separate traits of a species and its habitat use are explained *post hoc* or explanations focus on the relationship between a *single* species trait and a *single* environmental factor.

Most authors recognize, however, that causal mechanisms may be more complex and depend on multiple traits. They highlight the importance of considering trade-offs between traits and the functional equivalence of alternative suites of traits (Stearns, 1976; Resh *et al.*, 1994; Méricoux, Dolédec & Statzner, 2001). A specific combination of traits may be more adaptive than the constituent traits separately. For example, in a habitat with predictable but short periods of suitable conditions, the combination of rapid growth *and* obligate diapause provides an effective adaptation. Thus, for a given species, the adaptive value of a trait is context-dependent, being related to the remainder of its biology (Gould & Lewontin, 1979). Trait investment being constrained through trade-offs provides another example. Explicitly recognizing how species traits are interrelated may be more successful in unravelling the causal mechanisms underlying species-environment relationships.

In a previous paper (Verberk, Siepel & Esselink, 2008), we have defined life-history strategies for aquatic macroinvertebrates that take such aspects into account. We have based our strategies on interrelations between basic biological traits of species (known from life-history theory) and their functional implications. Life-history strategies may therefore present an integrated response to the environment. In this study, we test whether these theoretically derived life-history strategies can provide insight into how aquatic macroinvertebrates deal with the prevailing environmental conditions in existent waterbodies. Therefore, we apply life-history strategies to data gathered previously from various waterbodies. These waterbodies differ in species assemblages and environmental conditions (Verberk *et al.*, 2006). Thus, different ecological problems are present in each type of water body, and these differences are expected to be reflected in the abundance of (species exhibiting) different life-history strategies.

Methods

Study area and invertebrate sampling

The study was conducted in the Korenburgerveen nature reserve in the Netherlands (51°59'N; 6°39'E; 310 ha). The landscape of Korenburgerveen is

heterogeneous, consisting of a mosaic of different types of vegetation and transitions in between them. The present configuration of different types of vegetation is the result of both anthropogenic influences, such as peat cuttings and drainage, and spatial differences in the influence of ground water, surface water and rainwater, each with distinct chemical properties. In former peat cuttings in the western part and northern parts of the reserve, floating rafts of *Sphagnum* have established. In the higher parts, dry heather vegetations and dry forests with oak (*Quercus robur* Linnaeus) and birch (*Betula pendula* Roth) are present. In the lower parts, mesotrophic forests and fen vegetation are present, and locally great fen-sedge [*Cladium mariscus* (Linnaeus)] is abundant.

In total, 45 waterbodies were sampled. Thirty-seven waterbodies were sampled in both spring and autumn, six were sampled only in spring and two only in autumn. Waterbodies sampled only once were included in the analysis despite seasonal differences in species abundance (Verberk *et al.*, 2002). This is justified as the differences within a water body as a result of phenology are generally smaller than differences between waterbodies of a different type (see typology below) (Verberk *et al.*, 2005). Moreover, a preliminary analysis comparing samples taken in spring and autumn, showed seasonal differences to be negligible. All waterbodies sampled were small and isolated and generally unsuitable for fish (being acidic or temporary). Therefore they are considered to be fish-free, which was confirmed by the fact that no fish were captured or observed during sampling.

Macroinvertebrates were collected using a standard 30 × 20 cm pond net with a mesh size of 0.5 mm. Samples consisted of a sweep starting from the substratum and from more or less open water into denser vegetation near the shore. Further details on sampling method are given in Verberk *et al.* (2006). Samples were sorted in the laboratory. Tricladida, Hirudinea, Oligochaeta, Araneae, Crustacea, Odonata, Hemiptera (adults and nymphs), Ephemeroptera, Plecoptera, Megaloptera, Coleoptera (adults and larvae), Cylindrotomidae, Chaoboridae, Dixidae, Culicidae, Chironomidae, Ceratopogonidae and Trichoptera were identified to the lowest taxonomic level possible, which in most cases was to species.

Typology

A typology was constructed based on differences in environmental conditions (nutrient concentrations, acidity, alkalinity, soil type, dimensions, degree of shading and vegetation composition). A TWINSpan cluster analysis on environmental data with two cut-off levels divided the 45 sampled waterbodies in three main 'types' and eight 'subtypes' of water body. Prior to cluster analysis, redundancy among environmental factors was reduced by several principal component analyses (PCA). This condensed the environmental data into six principal component axes, representing the major environmental gradients (further details are given in Verberk *et al.*, 2006). A correspondence analysis (CA) of macroinvertebrate abundances transformed to a logarithmic scale based on the abundance classes of Preston (1962) shows a clear separation between the main types of water body, and also the different subtypes are separated (Fig. 1). The first two axes had high eigenvalues (0.42 and 0.39) and together explained 16.3% of the species data and 49.8% of the species-environment relationship.

The three main types of water body were bog pools, mesotrophic waters and waterbodies in wet forests, differing in physical and chemical properties (Table 1). The bog pools were mainly located on peat moss soils and had low pH, which is reflected in the positive correlation with the first chemical axis (Chem1), which represents differences in acidity (with high values indicating a high acidity, low alkalinity and low calcium concentrations). This gradient in acidity was also reflected in the first vegetation axis (Veg1), with low values corresponding to plant species such as *Sphagnum* spp, *Eriophorum angustifolium* Honckeny and *Andromeda polifolia* Linnaeus. The second chemical axis (Chem2) reflects differences in nutrients (with high values indicating low concentrations of nitrate and phosphate), which differed between the three subtypes of bog pool, along with differences in size, degree of shading and propensity to desiccation.

Waterbodies in wet forests were small and shallow and these properties are associated with high values of the first physical axis (Phys1). A high degree of shading and propensity to desiccation also characterize this type of water body and these properties are reflected in low values of Phys2. Despite some

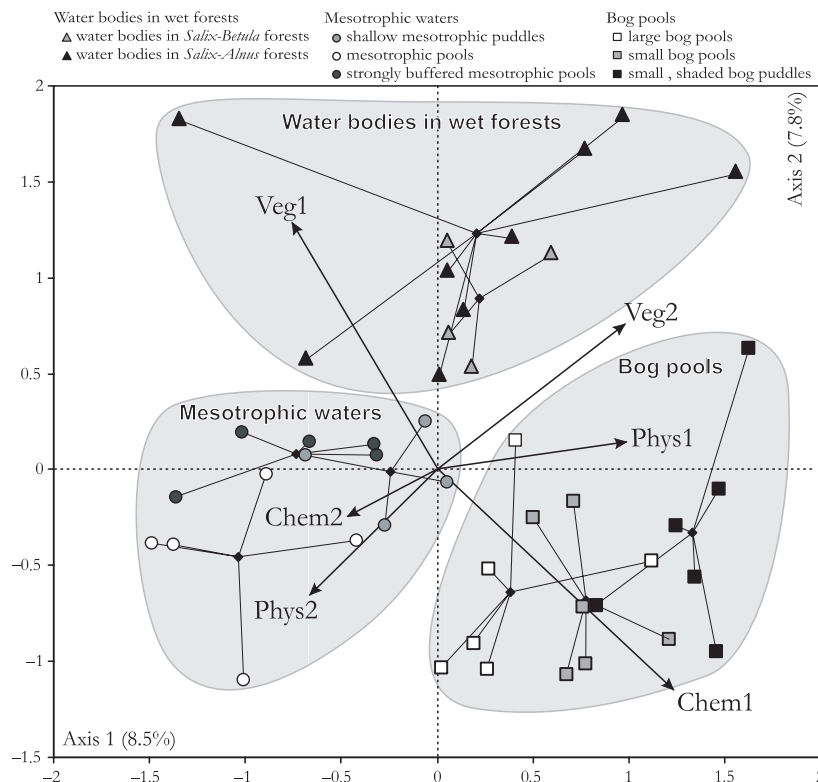


Fig. 1 Correspondence Analysis, showing the position of all sampled sites according to their species composition. Also shown are the six principal component axes, corresponding to the major environmental gradients (scores were multiplied by four for clarity). Axes describe differences in vegetation composition (Veg1 & Veg2), physical (Phys1 & Phys2) and chemical conditions (Chem1 & Chem2) between the different categories of waterbodies. The main environmental conditions condensed in each of these principal component axes are mentioned in the text.

variation in macroinvertebrate assemblage (Fig. 1), two subtypes were distinguished based on differences in environmental conditions, differing in pH and alkalinity as well as in nutrient concentrations (Table 1). Plant species such as *Alnus glutinosa* (Linnaeus), *Mentha aquatica* Linnaeus, *Riccia fluitans* Linnaeus and *Solanum dulcamara* Linnaeus were associated with the subtype of waterbodies in *Salix-Alnus* forest (high values of Veg1), whereas, *Rubus fruticosus* Linnaeus and *Dryopteris carthusiana* (Villars) were associated high values of Veg2.

Mesotrophic waterbodies were characterized by the occurrence of submerged and floating vegetation, with low values of Veg2 associated with plants such as *Potamogeton* spp. (*P. natans* Linnaeus and *P. polygonifolius* Pourret), *Potentilla palustris* (Linnaeus) and *Typha latifolia* Linnaeus. Mesotrophic waterbodies were relatively poor in nutrients (high values of Chem2) and mainly located on podzol soils (except for strongly buffered mesotrophic pools). Three

subtypes of mesotrophic waterbodies were distinguished, differing mainly in size, alkalinity and depth. The large mesotrophic waterbodies were deep, large and exposed to the sun (low degree of shading), which is also reflected in high values of Phys2.

Strategy assignment and data analysis

All 238 taxa collected were assigned to a life-history strategy, based on information regarding the species traits they possessed (see Fig. 2 for the main differences in species traits; Appendix S1 for sources of information and Appendix S2 for a list of species and their life-history strategy with examples of species assignment for the most abundant species). The approach of using life-history strategies rests on three principles. Firstly, species traits are interrelated, with investments in one trait, leaving fewer resources available for investments in another (trade-offs), or investments in one trait reducing costs (or increase

Table 1 Differences in physical and chemical conditions between the different water types. Means \pm standard error are shown

Main type	Water type	No. Water bodies	pH	Alkalinity (meq L ⁻¹)	o-PO ₄ ³⁻ (μ mol L ⁻¹)	NO ₃ ⁻ (μ mol L ⁻¹)	NH ₄ ⁺ (μ mol L ⁻¹)	Size (m ²)	Depth (cm)	Shading (%)	Temporary*
Mesotrophic waters	Shallow mesotrophic puddles	4	5.4 \pm 0.3	0.26 \pm 0.06	1.0 \pm 0.4	4.0 \pm 0.1	11.4 \pm 2.1	52 \pm 33	0.4 \pm 0.1	39 \pm 11	0.3 \pm 0.1
	Large mesotrophic pools	5	5.7 \pm 0.2	0.36 \pm 0.14	0.5 \pm 0.2	4.6 \pm 0.7	9.7 \pm 2.0	409 \pm 211	1.1 \pm 0.2	13 \pm 5	0 \pm 0
	Strongly buffered mesotrophic pools	5	6.5 \pm 0.2	1.06 \pm 0.18	1.3 \pm 0.5	2.1 \pm 0.3	8.0 \pm 1.0	108 \pm 42	0.7 \pm 0.1	39 \pm 14	0.2 \pm 0.1
Waterbodies in wet forests	Waterbodies in <i>Salix-Betula</i> forests	4	5.0 \pm 0.3	0.28 \pm 0.14	3.3 \pm 1.3	3.1 \pm 0.3	28.8 \pm 8.2	18 \pm 5	0.3 \pm 0.0	62 \pm 19	0.6 \pm 0.2
	Waterbodies in <i>Salix-Alnus</i> forests	9	6.2 \pm 0.2	1.69 \pm 0.33	1.3 \pm 0.4	32.7 \pm 19.7	41.3 \pm 15.9	24 \pm 6	0.3 \pm 0.1	61 \pm 13	0.3 \pm 0.1
Bog pools	Large bog pools	6	3.7 \pm 0.0	0.00 \pm 0.00	1.4 \pm 0.4	4.3 \pm 0.5	16.1 \pm 5.5	34 \pm 14	0.5 \pm 0.2	27 \pm 8	0.0 \pm 0.0
	Small bog pools	6	3.8 \pm 0.1	0.00 \pm 0.00	1.0 \pm 0.2	4.8 \pm 0.5	40.9 \pm 12.4	16 \pm 8	0.5 \pm 0.1	37 \pm 8	0.2 \pm 0.2
	Small, shaded bog puddles	6	3.8 \pm 0.1	0.00 \pm 0.00	1.6 \pm 0.4	12.3 \pm 5.3	44.7 \pm 11.7	8 \pm 4	0.5 \pm 0.2	66 \pm 16	0.2 \pm 0.2

*Indicating the propensity to desiccation of a water body, ranging from 0 (permanent) to 1 (temporary).

benefits) for investments in another (spin-offs). Secondly, the adaptive value and whether or not a species trait is strongly pronounced is dependent on the context of the remainder of a species' life-history and its body plan. Additionally, given that high investment in one trait constrains investment in another, high investments are probably selected against unless they enhance survival. Thirdly, and finally, by focussing on the adaptive value of combinations of traits (rather than on the identity of separate traits), different suites of traits may be equivalent, presenting a similar solution to an ecological problem. Based on these principles, thirteen life-history strategies have been defined in a previous paper (Verberk *et al.*, 2008).

Below we briefly outline the differences in species trait investments for each life-history strategy and its putative relationship with the environment. Species that invest strongly in dispersal, and have a rapid juvenile development, usually also have long-lived adults that feed (strategy D1). By protracting the oviposition period, species can feed between bouts of oviposition and thus increase the *per capita* investment (strategy R1). Their dispersal and protracted oviposition enable these species to exploit suitable conditions if some spatio-temporal variation exists (i.e. it pays off to disperse). At a lower *per capita* investment, juvenile development takes longer, but a larger clutch size is permitted (strategy D2). By further increasing reproductive effort and dispersal at the cost of adult longevity these species can effectively exploit conditions which are suitable for a longer time, but situated at large spatial distances. The alternative of shortening development time, constraining reproduction and adult longevity, enables a higher voltinism (strategy D3), which can be of adaptive advantage when conditions frequently become briefly suitable at different places. For species without active dispersal, a similar dichotomy between a low *per capita* investment, univoltine life-history (strategy R2), and a high *per capita* investment, multivoltine life-history (strategy R3) can be discerned. More importance is placed on persistence in these strategies as recolonization is more difficult. A high rate of increase enables a rapid expansion following a local disturbance. Hermaphroditic and asexual reproduction (strategy R4) further increase a species' rate of increase and resistant stages enhance survival during (periodic) disturbances.

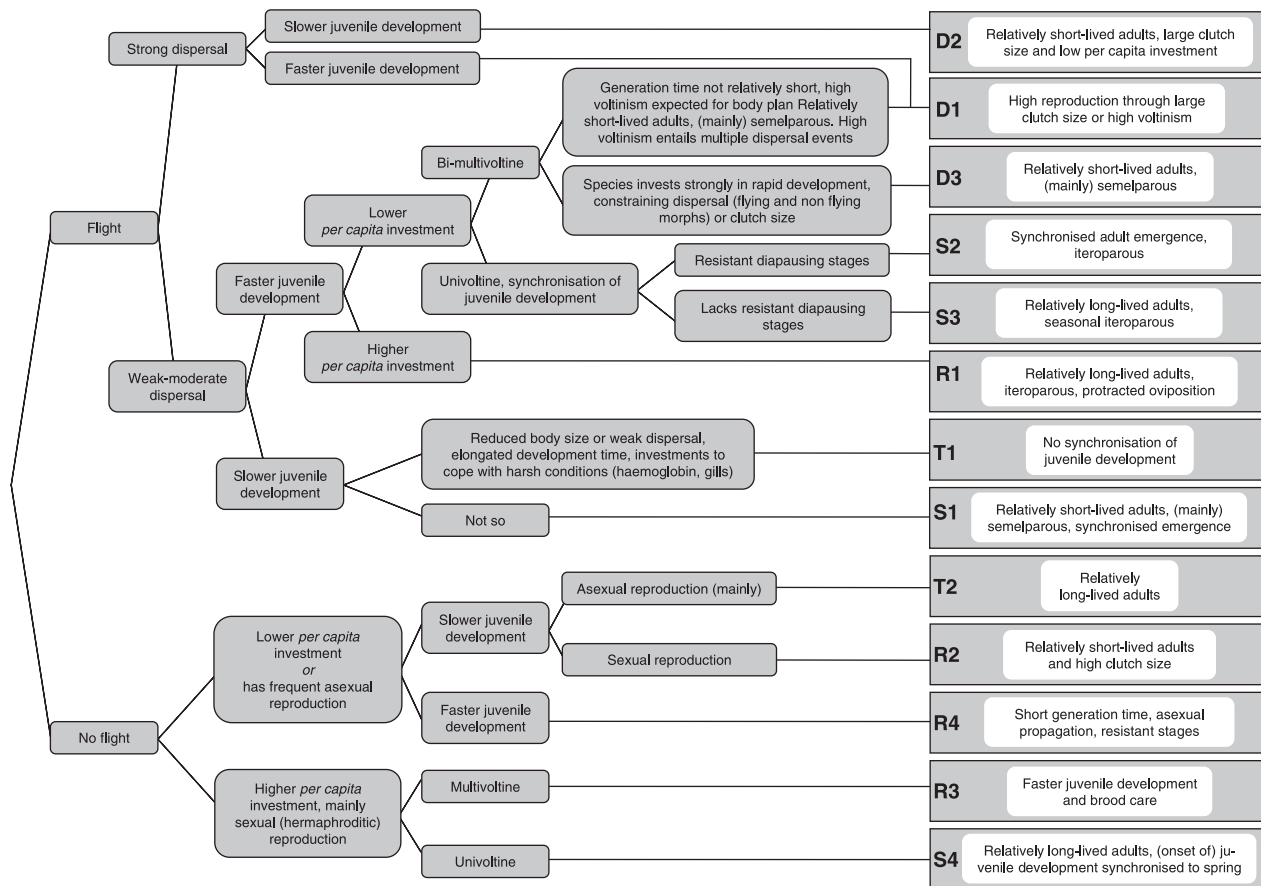


Fig. 2 Overview of the different life-history strategies and their defining species traits. Differences in investments in traits refer to relative rather than absolute values and were interpreted relative to the remainder of a species' life-history, body plan and feeding guild. See Appendix S1 for sources of information and Appendix S2 for a list of species and their life-history strategy with examples of species assignment for the most abundant species.

Species with a long period of juvenile development can have short-lived adults, if their emergence is synchronized (strategy S1). The onset of juvenile growth can also be synchronized to periods of suitable conditions either with a diapausing, resistant stage to survive intermittent hostile conditions (strategy S2) or not (strategy S3). These synchronization strategies work best under predictable conditions. Species without active dispersal and a high *per capita* investment can synchronize the onset of juvenile development by synchronizing reproduction (strategy S4). High investments in physiological and morphological adaptations (e.g. haemoglobin, gills) to combat environmental hardship constrain reproduction, dispersal and body size (strategy T1), but confers a high tolerance for abiotic extremes. Species with such adaptations, but lacking active dispersal usually

reproduce asexually (strategy T2) and are best suited to harsh and constant conditions.

Data analysis

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 strategy were pooled. Differences in the strategies (summed percentages) were tested statistically for the three main water types, but not for the eight subtypes, due to the low number of replicate waterbodies within each subtype. For each strategy, differences in the proportion of a strategy (expressed as a percentage) between the three main

types were tested non-parametrically using a Kruskal–Wallis test.

Results

Most strategies were represented by species from different systematic groups and different strategies were represented within a systematic group (Table 2). Systematic groups with many different aquatic species also included more strategies. Strategies S4, R2, R3, R4 and T2 occurred mainly in non-insect groups, including leeches, triclads and worms, reflecting differences in their body plan. These groups lack active flight and have hermaphroditic and asexual reproduction. In insects, the number of species representing the various strategies differed between the systematic groups, but without consistent differences between for example holometabolous and hemimetabolous insects. Species assigned to strategies D1, S2, S3, R1 and T1 belonged to systematic groups with many aquatic species (Diptera, Coleoptera, Odonata, Hemiptera and Trichoptera; Table 2) and consequently these strategies were represented by many species (Fig. 3). Relative to the number of species, strategies with a potentially high intrinsic rate of increase (due to short generation time or hermaphroditic or asexual reproduction; strategies R3, R4 and T2) were strongly represented numerically, which is reflected in higher densities (Fig. 3).

The percent composition of the strategies differed strongly between the eight different subtypes in the

study area (Fig. 4). Also, when subtypes were aggregated, significant differences between the three main water types were found for eight strategies (Fig. 5). In the shallow mesotrophic puddles, species with a high tolerance for unfavourable conditions (strategy T1) and without active dispersal (strategies R3, R4 and T2) were abundant. In the larger and more stable mesotrophic pools, species with a long period of juvenile development and a synchronized emergence of short-lived adults (strategy S1) were very abundant in combination with species in strategy T1. Species with strong active dispersal and a high clutch size (strategy D2) were abundant in both the large mesotrophic pools and the strongly buffered mesotrophic pools. In contrast, species that have a fast development and spread successive reproductive attempts over a longer time period (strategy R3) were scarce in the large mesotrophic pools but abundant in the strongly buffered mesotrophic pools. Species in strategy R3 were also very abundant in the waterbodies in wet forests (Fig. 5). Species in strategy S1, R1 and T2 were more abundant in *Salix-Alnus* forests compared to *Salix-Betula* forests. In the bog pools, species in strategy T1 and S1 were most abundant, whereas species in strategy D2, R3 and R4 were largely absent (Fig. 5). Species in strategy T1 were represented by different species in the different types of bog pools (Fig. 6). Large bog pools show high abundance of *Ceragrion tenellum* (de Villers) and *Argyroneta aquatica* (Clerck), while small, shaded bog puddles showed high densities of *Polypedilum uncinatum* agg. and

Table 2 Number of species in a systematic group and their distribution over the life-history strategies. The number of life-history strategies for each systematic group is indicated between brackets. Taxon names are given in Appendix S1

		Life-history strategy													
Systematic group	Total	D1	D2	D3	S1	S2	S3	S4	R1	R2	R3	R4	T1	T2	
Arachnida	1 (1)												1		
Coleoptera	86 (7)	22			2	8	22		19				12	1	
Crustacea	1 (1)										1				
Diptera	64 (6)	15		9	13	6			2				19		
Ephemeroptera	1 (1)		1												
Hemiptera	20 (4)	6		3					7				4		
Hirudinea	6 (3)							2		2	2				
Megaloptera	1 (1)												1		
Odonata	15 (4)		3		2	4							6		
Oligochaeta	23 (3)							9				8		6	
Plecoptera	1 (1)												1		
Trichoptera	15 (4)	1			2	7							5		
Tricladida	4 (2)							2		2					
Total	238 (13)	44	4	12	19	25	22	13	28	4	3	8	49	7	

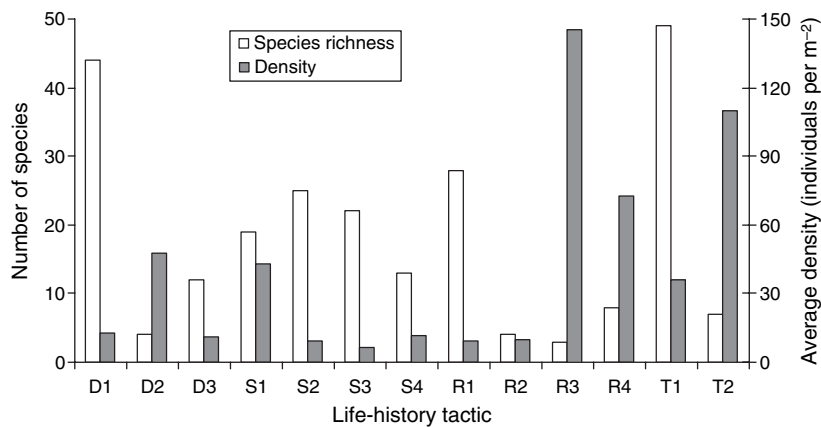


Fig. 3 Number of species and density for each life-history strategy. Average densities were calculated for each species (individuals per m⁻², averaged across all sites where it was present) and subsequently averaged for species in the same strategy. The defining species traits for each strategy are shown in Fig. 2.

Cyphon sp. Tolerant species without dispersal (strategy T2) increased from large bog pools to small and shaded bog puddles (Fig. 4). Concomitantly, there was a shift from strategy S3 to S2.

Discussion

The goal of this paper was to test whether theoretically derived life-history strategies can provide insight into how aquatic macroinvertebrates deal with the prevailing environmental conditions in different categories (types and subtypes) of water body. Since, within a given category, a multitude of environmental conditions acts in concert, we examined patterns in life-history strategies across categories, rather than rearranging data according to gradients of single environmental factors. In our analyses we focussed on species abundance rather than species richness. Differences in strategy composition based on number of individuals (Fig. 3) reflected characteristics of the strategies, such as the intrinsic rate of increase, while differences based on the number of species reflected differences in species richness between systematic groups. Thus, a strategy that is here represented by many individuals can be considered an ecologically successful strategy for the lentic waterbodies studied here. Conversely, the number of species exhibiting a given strategy could be considered to be a measure of the latter's evolutionary success, but this will require a broader perspective than the lentic waterbodies studied here. To examine patterns in life-history strategies across categories of water body, individuals were

therefore considered to be a more straightforward unit than species.

Patterns in life-history strategies

Patterns in life-history strategies differed among the categories of water body (Figs 3 & 4). Differences in species traits among life-history strategies and differences in environmental conditions among waterbodies could explain these patterns. The different waterbodies could be schematically placed along two axes representing habitat suitability and habitat predictability (Fig. 7). In the acid bog pools species with a high tolerance for harsh conditions were favoured (strategy T1). These species invested less in reproduction and dispersal and were less abundant under more benign conditions (richer in nutrients, less acid) found in waterbodies in wet forests and strongly buffered mesotrophic pools. The harsh conditions in bog pools also explained the absence of species following a resource dominance strategy (strategies D2, R3 and R4). Bog puddles represented the most harsh subtype, due to low temperatures (high shading) constraining development and a larger impact of drought (smaller size). These conditions favour both species that are very tolerant (strategy T2) and species with resistant stages (S2) over species without such resistant stages (S3).

Large mesotrophic pools represented a very stable and benign environment (no food shortage, low acidity, high oxygen). These conditions favour species that have a long juvenile development period (strat-

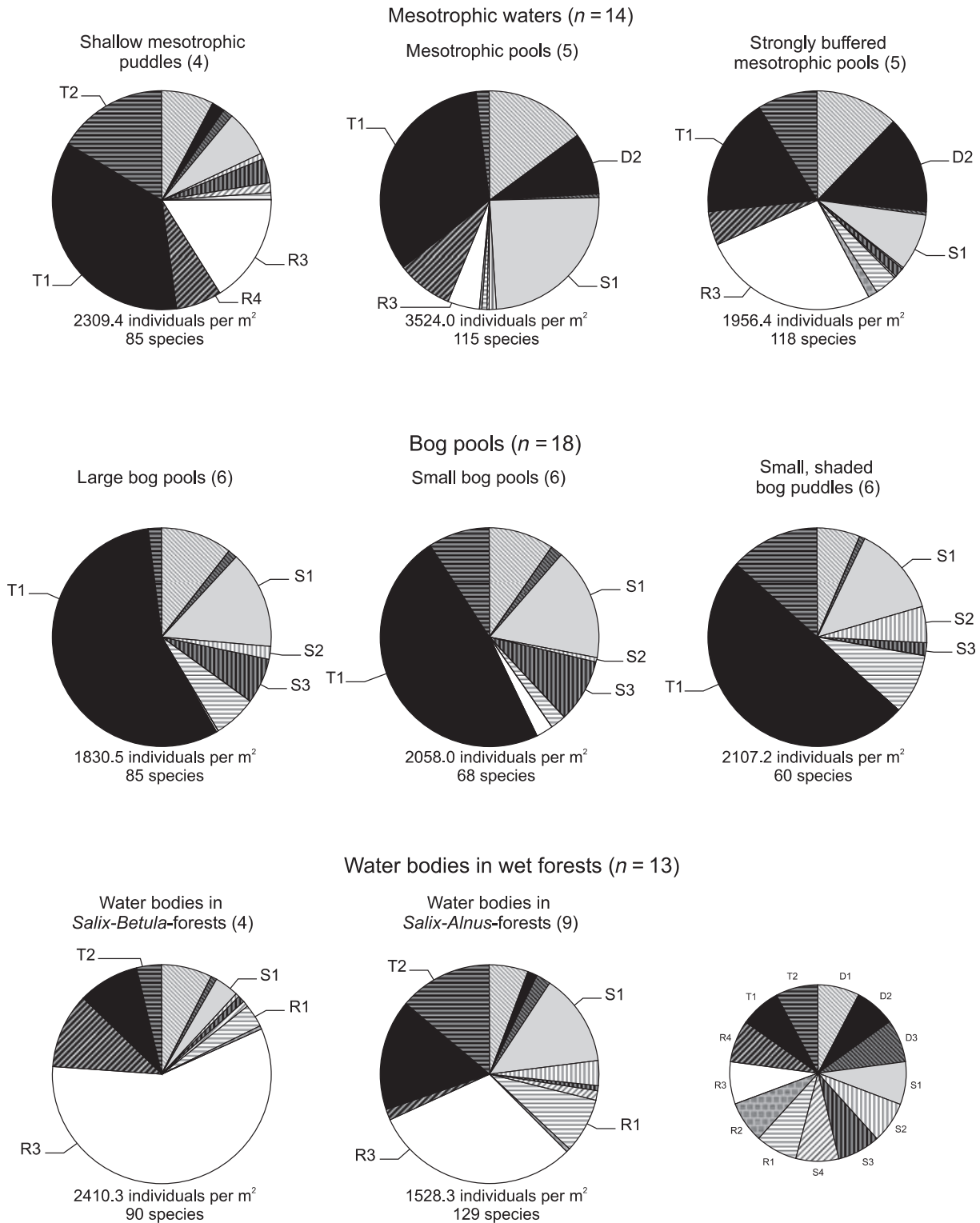


Fig. 4 Proportion of life-history strategies in each of the eight subtypes of water body. Percentages are averaged for waterbodies of the same type. The number of waterbodies is given in parentheses and, for each subtype, mean density and species richness are listed. Different strategies are indicated with different shadings (see key bottom right) and those mentioned in the text are labelled separately. The defining species traits for each strategy are shown in Fig. 2.

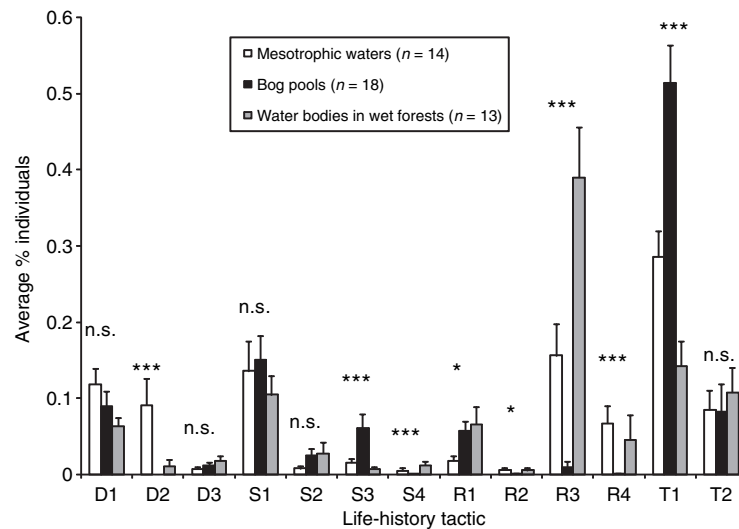


Fig. 5 Proportion of life-history strategies (expressed as percentages \pm SE) in each of the three main types of water body. Percentages are averaged for waterbodies of the same water type. The number of waterbodies is given within brackets. Asterisks indicate significant differences (Kruskal–Wallis test): n.s.: $P > 0.05$; * $P < 0.05$; *** $P < 0.001$. The defining species traits for each strategy are shown in Fig. 2.

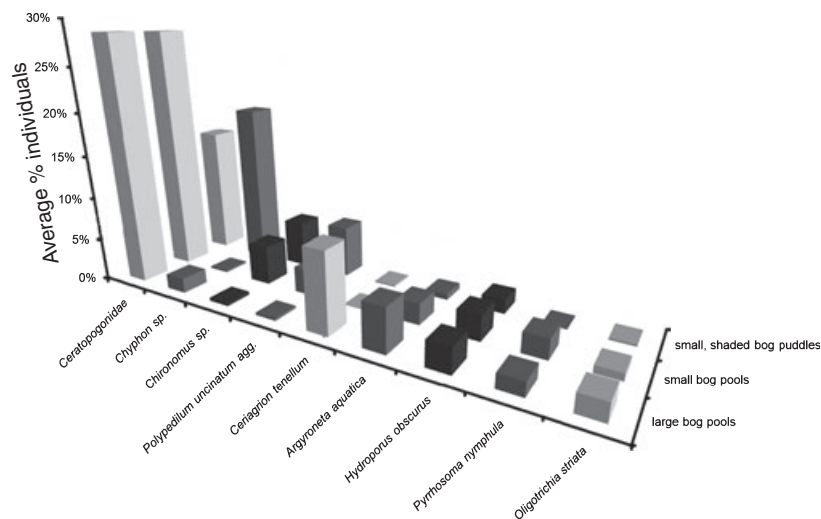


Fig. 6 Proportion of the nine most abundant taxa assigned to life-history strategy T1 in the bog pools.

egies T1 and S1) and a low *per capita* investment in offspring (strategy D2). Species in strategy S1 have a synchronized life cycle with short-lived adults and require predictable conditions for their larval development. Such predictable conditions are provided in the large mesotrophic pools but to some extent, also in the harsher bog pools. Species in strategy D2 invest in a high clutch size and adult dispersal, which is coupled with a low *per capita* investment and for their juvenile development these species require a higher productivity and temperature. These conditions were

met in both the large and the strongly buffered mesotrophic pools, but not in the shaded waterbodies in wet forests. The acid, shallow mesotrophic puddles were susceptible to fluctuations in water level, but were unlikely to dry out completely. Under these conditions species invested in tolerating harsh conditions, while investment in dispersal was needed less. To compensate for their low dispersal capacity, many species had a resource dominance strategy, having a potentially high intrinsic rate of increase through hermaphroditic and asexual reproduction (strategies

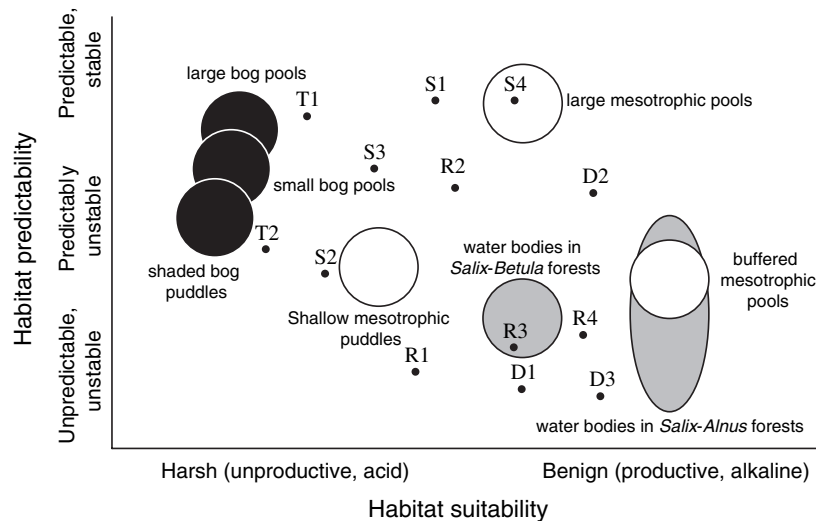


Fig. 7 Conceptual model based on Fig. 4, showing the position of the different categories of water body (open ovals: mesotrophic waters; dark grey ovals: bog pools; light grey ovals: waterbodies in wet forests) along two axes representing habitat suitability and predictability. The position of life-history strategies is also shown, reflecting both the proportions found in the different categories of water body (see Figs 4 & 5) and (especially for the strategies with low proportions) and their putative relations to habitat suitability and predictability. The defining species traits for each strategy are shown in Fig. 2.

R3, R4 and T2). Species in strategy R4 maximize their rate of increase through minimizing their age at first reproduction, which works best under more productive conditions. Species in strategy T2 are very tolerant to harsh conditions and are therefore expected to reach high abundance under different conditions than species in strategy R4. The shallow mesotrophic puddles were located in an area where there was occasionally an input of eutrophic surface water. In addition, these waterbodies were located on permeable soils and may have alternated between seepage and infiltration, as a result of the seasonal fluctuations in ground water influence. Such temporal fluctuations in environmental conditions favour sedentary species able quickly to exploit these new conditions, explaining the high abundance of species in both strategy R4 and strategy T2.

When conditions are suitable for a short or unknown period, rapid development is favoured, requiring a higher *per capita* investment. When conditions are more predictably of short duration, a short synchronized juvenile development in combination with resistant stages (strategy S2) is favoured. Waterbodies in small bog puddles, in which species in strategy S2 were abundant also had a high abundance of species in strategy R1. Species in this strategy have long lived adults capable of dispersal, enabling them to survive the unsuitable periods elsewhere. This

strategy thus represents an alternative solution to surviving unsuitable periods. Waterbodies in forests were most variable in terms of fluctuations in water level. Waterbodies in *Salix-Betula* forests were most susceptible to drying out, but the soil will have remained moist as the waterbodies were located on peat moss soils. With a large influence of precipitation, the occurrence and duration of suitable conditions is unpredictable in these waterbodies. Under such unpredictable conditions, species are favoured that have a rapid development and spread successive reproductive attempts over a long time period (strategy R3). As waterbodies in *Salix-Alnus* forests had more seepage, the predictability of suitable conditions was higher, favouring species in strategy S1. More alkaline conditions also increase decomposition which causes periods of hypoxia, favouring tolerant species in strategy T1 and T2 and species capable of surviving unsuitable periods elsewhere (strategy R1).

Merits of life-history strategies

In this study, we have provided mechanistic explanations linking two data-sets of different origin, on the one hand involving data from literature on the biology of the various species (condensed into life-history strategies, see Verberk *et al.*, 2008) and on the other hand field data on both species occurrences and

environmental conditions (described in Verberk *et al.*, 2006). Life-history strategies provided a functional classification of macroinvertebrates spanning different systematic groups (Table 2). Different species have different species traits but may be assigned to the same life-history strategy, provided that the combination of species traits solves problems for survival in a similar way.

Many studies that relate species traits to patterns in habitat use, employ multivariate analytical techniques in which species traits are weighted equally (i.e. independent from other traits possessed). In such analyses, trait-environment relationships are averaged across all species. As a result, the importance of some traits may be masked (Van Kleef *et al.*, 2006) and the magnitude of differences among traits is often very small, even if highly significant (Townsend, Dolédec & Scarsbrook, 1997; Statzner *et al.*, 2001). When combining species traits into life-history strategies, larger differences can be found. For example, differences between types of waterbodies for a given strategy ranged up to 38% (58% between subtypes of water body) and differences with respect to a combination of strategies were even higher, with (Bray-Curtis) dissimilarity coefficients ranging up to 50% (72% for subtypes). However, when considering waterbodies of the same category, differences in percentage composition of strategies were relatively small or involved shifts between functionally similar strategies. More important than the magnitude of differences is the fact that connecting species traits based on knowledge from life-history theory allows a better linkage between species traits and the causal mechanisms underlying species-environment relationships. For example, multivariate analyses by Van Kleef *et al.* (2006) did not reveal flight capability to be important in the recolonization of shallow lakes. This counterintuitive result arose because many species with active flight were *also* carnivorous and their recolonization was delayed due to the scarcity of prey.

Life-history strategies reflect patterns of investment in species traits that are expected to solve problems for survival, as evolution has influenced the energy allocation through trade-offs, spin-offs and body plan constraints. By providing a framework of causal mechanisms, patterns in strategy composition across water types could be explained in terms of to the prevailing environmental conditions governing habitat suitability and predictability (Fig. 7), supporting

Southwood's (1977) habitat templet concept. The intimate relation between life history-strategies and causal mechanisms has several advantages.

Firstly, it is possible to aggregate information across species and across strategies by looking at the function of species traits in dealing with ecological problems. For example, differences in the abundance of individual species in each type of bog pool, could be largely aggregated to a single strategy (T1), indicating that many species from different systematic groups perceived the prevailing conditions as harsh (Fig. 6). Additionally, some responses were manifested across multiple strategies, as a particular problem can be solved by different strategies, or conversely, strategies presented such opposing solutions that they almost excluded one another. For example, strategies S2 and R1, and strategies D2 and R4, were positively correlated (Spearman $r = +0.44$; $P = 2.6 \times 10^{-3}$ and Spearman $r = +0.76$; $P = 1.0 \times 10^{-6}$, respectively), whilst strategies T1 and R3 were negatively correlated (Spearman $r = -0.71$; $P = 1.0 \times 10^{-6}$). Thus, the combination of strategies in a particular category of water body will be most informative.

Secondly, more traditional assessment methods do not have straightforward relations to mechanistic explanations underpinning patterns in species occurrence (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 (Grime, 1977; Huston, 1979) and may vary with scale (Chase & Leibold, 2002). Rapid assessments using multivariate analytical techniques and assessments employing multi metrics are usually not related *a priori* to ecological quality. 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 ecological quality and its impairment, involves equally complex descriptions of reference conditions, which are used for calibration (Reynoldson *et al.*, 1997; Chessman, 1999; Bates Prins & Smith, 2007). Thus, with simple indices, too little information is taken into account or remains after aggregating complex information into a single index. In contrast, with more advanced and complex methods too much information is generated, resulting from a failure to identify key mechanistic explanations underpinning patterns in species occurrence. The use

of life-history strategies reduces the vast complexity of many species belonging to many different systematic groups to a small number of strategies (although species identification remains necessary). These strategies have functional relationships with the duration, degree and predictability of habitat suitability in space and time. They may provide useful elements for biomonitoring, not so much in establishing reference values for the expected strategy composition of intact and degraded systems, but rather by providing insight as to which pressures should be addressed to improve ecological quality.

Thirdly and finally, by providing mechanistic explanations, life-history strategies 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. For example, eutrophication of raised bogs (Van Duinen *et al.*, 2006) has resulted in the combination of high acidity and high nutrient availability, which did not exist in the past.

In conclusion, life-history strategies integrate information on the biological traits and habitat use of species to derive the most likely explanations and generate testable hypotheses. The distribution of species numbers over the various life-history strategies in a location gives direct information about how a particular environment is experienced by the species present. Therefore, life-history strategies may focus subsequent research efforts and management efforts. Extending our approach to other freshwater ecosystems (*e.g.* running waters), and incorporating other systematic groups (*e.g.* fish, plants, zooplankton) may reveal new life-history strategies.

Acknowledgments

We would like to thank Rob Leuven, Gerard van der Velde and Piet Verdonchot for valuable comments on earlier drafts. Joana Frazão assisted in the compilation of available data on the ecology of Hemiptera. Henk Moller-Pillot provided all data on Chironomidae, and supplemented the data on Hemiptera. Tarmo Timm supplemented the data on the aquatic Oligochaeta. Bert Higler supplemented the data on Trichoptera. Jan Cuppen supplemented the data on aquatic beetles and confirmed a number of species

identifications. Two anonymous reviewers provided useful comments on the manuscript.

References

- Bates Prins S.C. & Smith E.P. (2007) Using biological metrics to score and evaluate sites: a nearest-neighbour reference condition approach. *Freshwater Biology*, **52**, 98–111.
- Bonada N., Prat N., Resh V.H. & Statzner B. (2006) Developments in aquatic insect biomonitoring: a comparative analysis of recent approaches. *Annual Review of Entomology*, **51**, 495–523.
- Bradshaw A.D. (1996) Underlying principles of restoration. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**(suppl. 1), 3–9.
- Bremner J., Rogers S.I. & Frid C.L.J. (2006) Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecological Indicators*, **6**, 609–622.
- Chase J.M. & Leibold M.A. (2002) Spatial scale dictates the productivity-biodiversity relationship. *Nature*, **416**, 427–430.
- Chessman B.C. (1999) Predicting the macroinvertebrate faunas of rivers by multiple regression of biological and environmental differences. *Freshwater Biology*, **41**, 747–757.
- Finn D.S. & Poff N.L. (2005) Variability and convergence in benthic communities along the longitudinal gradients of four physically similar Rocky Mountain streams. *Freshwater Biology*, **50**, 243–261.
- Gayraud S., Statzner B., Bady P., Haybach A., Schöll F., Usseglio-Polatera P. & Bacchi M. (2003) Invertebrate traits for the biomonitoring of large European rivers: an initial assessment of alternative metrics. *Freshwater Biology*, **48**, 2045–2064.
- Gould S.J. & Lewontin R.C. (1979) The Spandrels of San Marco and the panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **205**, 581–598.
- Grime J.P. (1977) Evidence for existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, **111**, 1169–1194.
- Hobbs R.J. & Norton D.A. (1996) Towards a conceptual framework for restoration ecology. *Restoration Ecology*, **4**, 93–110.
- Huston M. (1979) A general hypothesis of species diversity. *The American Naturalist*, **113**, 81–101.
- Ilg C. & Castella E. (2006) Patterns of macroinvertebrate traits along three glacial stream continuums. *Freshwater Biology*, **51**, 840–853.

- Jansson R., Backx H., Boulton A.J., Dixon M., Dudgeon D., Hughes F.M.R., Nakamura K., Stanley E.H. & Tockner K. (2005) Stating mechanisms and refining criteria for ecologically successful river restoration: a comment on Palmer *et al.* *Journal of Applied Ecology*, **42**, 218–222.
- Keddy P.A. (1992) A pragmatic approach to functional ecology. *Functional Ecology*, **6**, 621–626.
- McGill B.J., Enquist B.J., Weiher E. & Westoby M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, **21**, 178–185.
- Mérigoux S., Dolédec S. & Statzner B. (2001) Species traits in relation to habitat variability and state: neotropical juvenile fish in floodplain creeks. *Freshwater Biology*, **46**, 1251–1267.
- Mouillot D., Spatharis S., Reizopoulou S., Laugier T., Sabetta L., Basset A. & Chi T.D. (2006) Alternatives to taxonomic-based approaches to assess changes in transitional water communities. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **16**, 469–482.
- Nijboer R.C. (2006) *The Myth of Communities. Determining Ecological Quality of Surface Waters Using Macroinvertebrate Community Patterns*. PhD Thesis, Alterra Scientific Contributions 17, Alterra, Wageningen.
- Preston F.W. (1962) The canonical distribution of commonness and rarity: part 1. *Ecology*, **43**, 185–215.
- Resh V.H., Hildrew A.G., Statzner B. & Townsend C.R. (1994) Theoretical habitat templates, species traits, and species richness - a synthesis of long-term ecological research on the upper Rhône river in the context of currently developed ecological theory. *Freshwater Biology*, **31**, 539–554.
- Reynoldson T.B., Norris R.H., Resh V.H., Day K.E. & Rosenberg D.M. (1997) The reference condition: a comparison of multimetric and multivariate approaches to assess water-quality impairment using benthic macroinvertebrates. *Journal of the North American Benthological Society*, **16**, 833–852.
- Rosenberg D.M. & Resh V.H. (1993) *Freshwater Biomonitoring and Benthic Macroinvertebrates*. Chapman & Hall, New York.
- Southwood T.R.E. (1977) Habitat, the templet for ecological strategies? *Journal of Animal Ecology*, **46**, 337–365.
- Statzner B., Resh V.H. & Dolédec S. (1994) Ecology of the upper Rhône river: a test of habitat templet theories. *Freshwater Biology*, **31**, 253–554.
- Statzner B., Bis B., Dolédec S. & Usseglio-Polatera P. (2001) Perspectives for biomonitoring at large spatial scales: a unified measure for the functional composition on invertebrate communities in European running waters. *Basic and Applied Ecology*, **2**, 73–85.
- Stearns S.C. (1976) Life-history tactics: a review of the ideas. *Quarterly Review of Biology*, **51**, 3–47.
- Thorne R.S.J. & Williams W.P. (1997) The response of benthic macroinvertebrates to pollution in developing countries: a multimetric system of bioassessment. *Freshwater Biology*, **37**, 671–686.
- Townsend C.R., Dolédec S. & Scarsbrook M.R. (1997) Species traits in relation to temporal and spatial heterogeneity in streams: a test of habitat templet theory. *Freshwater Biology*, **37**, 367–387.
- Usseglio-Polatera P., Bournaud M., Richoux P. & Tachet H. (2000) Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. *Freshwater Biology*, **43**, 175–205.
- Van Duinen G.A., Timm T., Smolders A.J.P., Brock A.M.T., Verberk W.C.E.P. & Esselink H. (2006) Differential response of aquatic oligochaete species to increased nutrient availability – a comparative study between estonian and dutch raised bogs. *Hydrobiologia*, **564**, 143–155.
- Van Kleef H.H., Verberk W.C.E.P., Leuven R.S.E.W., Esselink H., van der Velde G. & van Duinen G.A. (2006) Biological traits successfully predict the effects of restoration management on macroinvertebrates in shallow softwater lakes. *Hydrobiologia*, **565**, 201–216.
- Verberk W.C.E.P., Siepel H. & Esselink H. (2008) Life-history strategies in freshwater macroinvertebrates. *Freshwater Biology*, **53**, 1722–1738.
- Verberk W.C.E.P., Van Kleef H.H., Dijkman M., Van Hoek P., Spierenburg P. & Esselink H. (2005) Seasonal changes on two different spatial scales: response of aquatic invertebrates to water body and microhabitat. *Insect Science*, **12**, 263–280.
- Verberk W.C.E.P., van Duinen G.A., Brock A.M.T., Leuven R.S.E.W., Siepel H., Verdonchot P.F.M., van der Velde G. & Esselink H. (2006) Importance of landscape heterogeneity for the conservation of aquatic macroinvertebrate diversity in bog landscapes. *Journal for Nature Conservation*, **14**, 78–90.
- Verberk W.C.E.P., Brock A.M.T., van Duinen G.A., van Es M., Kuper J.T., Peeters T.M.J., Smits M.J.A., Timan L. & Esselink H. (2002) Seasonal and spatial patterns in macroinvertebrate assemblage in a heterogeneous landscape. *Proceedings of the Section Experimental and Applied Entomology of the Netherlands Entomological Society (NEV)*, **13**, 35–43.
- Verdonchot P.F.M. (2000) Integrated ecological assessment methods as a basis for sustainable catchment management. *Hydrobiologia*, **422/423**, 389–412.
- Wallace J.B., Grubaugh J.W. & Whiles M.R. (1996) Biotic indices and stream ecosystem processes: results from an experimental study. *Ecological Applications*, **6**, 140–151.

- Weiner J. (1995) On the practice of ecology. *Journal of Ecology*, **83**, 153–158.
- Whitehurst I.T. (1991) The *Gammarus-Asellus* ratio as an index of organic pollution. *Water Research*, **25**, 333–339.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Main sources of information on biological traits for the species captured in this study. Data were supplemented by the following experts: J.G.M. Cuppen (Coleoptera), L.W.G. Higler (Trichoptera), H.K.M. Moller-Pillot (Chironomidae & Hemiptera) and T. Timm (Oligochaeta).

Appendix S2. List of taxa captured and their life-history strategy. For each strategy, the rationale behind the assignment of is given for a few abundant species in footnotes. These species made up more than 50% of the total number of individuals. The defining species traits for each strategy are shown in Fig. 2.

Please note: Blackwell Publishing are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

(Manuscript accepted 11 May 2008)