Theoretical habitat templets, species traits, and species richness: Plecoptera and Ephemeroptera in the Upper Rhône River and its floodplain

PHILIPPE USSEGLIO-POLATERA*[†] AND HENRI TACHET[‡]

* *Centre de Recherches Ecologiques, Université de Metz, BP 4116, 57040 Metz Cedex 01, France*
[‡] *URA CNRS 1451 'Ecologie des Eaux Douces et des Grands Fleuves', Université Lyon I, 69 622 Villeurbanne Cedex, France*

[†] *Author to whom correspondence should be sent*

SUMMARY

1. Ephemeroptera and Plecoptera in two sites of the Upper Rhône River (France) were examined using multivariate analyses to determine: (i) relationships among seventeen species traits; (ii) habitat utilization of the fifty-five species present; (iii) the relationship between species traits and habitat utilization; (iv) trends of species traits and species richness in a framework of spatial and temporal habitat variability.
2. The species traits having the highest correlation ratios correspond to reproduction or life cycle, behavioural, and morphological characteristics. According to their traits, species of Baetidae, Caenidae, and Leptophlebiidae (Ephemeroptera) are opposite species of Perlidae and Perlodidae (Plecoptera).
3. The distribution of species in thirteen habitat types of the Upper Rhône River floodplain demonstrates a transverse gradient from the main channel to the oxbow lakes. Plecoptera are restricted to the different main channel habitats; in contrast, Ephemeroptera families have a broader distribution with Baetidae and Leptophlebiidae occurring in most floodplain habitats.
4. Plecoptera exhibit a significant relationship between species traits and habitat utilization but no relationship is evident for Ephemeroptera. Baetidae use many habitat types and have diverse species traits; in contrast, Leptophlebiidae, Heptageniidae, and Caenidae use many habitat types but each family has a rather uniform set of traits.
5. Trends in species traits were significantly related to both the spatial and temporal variability of habitats. Considering only temporal variability, the distribution of species trait modalities (= categories) corresponded well to predictions on trends in the river habitat templet for 'minimum age at reproduction' and 'potential longevity', and in general for 'descendants per reproductive cycle', 'reproductive cycles per year', 'potential size', and 'body flexibility'; trends in six other traits did not match predictions.
6. No trends in species richness were evident in spatial–temporal framework of habitat variability.

Introduction

An aquatic ecosystem may be envisioned as a mosaic of patches, each of which is characterized by different environmental conditions. Patches that have a number of environmental conditions in common are usually termed habitats. In their development of habitat templets and their possible application to the study of aquatic benthic communities, Southwood (1977, 1988), Hildrew & Townsend (1987), Townsend (1989), and Townsend & Hildrew (1994) focused on the premise that the habitat provides the templet on which evolution forges characteristic life history strategies. The patch dynamics concept, applied to

lotic ecosystems by Pringle *et al.* (1988) and Townsend (1989), attempts to explain the organization of aquatic communities through different ecological concepts that emphasize the role of deterministic interactions between species (e.g. predation, competition) or stochastic factors (e.g. disturbances) that control community structure.

There has been an intuitive acknowledgement that the faunistic assemblage of a river ecosystem integrates the spatial and temporal variability of the habitat. Therefore, species with certain combinations of adaptations, especially traits related to survival and reproduction, are assumed to be selected for (Southwood, 1988). Consequently, to explain the local distribution of aquatic organisms, which is a central aim of ecology, we must study the link between species traits and environmental variability. If population dynamics can be assumed to be governed essentially by autecological processes (Townsend & Hildrew, 1994), the dynamics of communities in the framework of spatial and temporal variability may be predicted from the knowledge of the species traits of the faunistic assemblage. Synthesis of autecological information of macroinvertebrate species based on published accounts can be used for some of these species traits (Usseglio-Polatera, 1993). Usseglio-Polatera (1991) and Bournaud, Richoux & Usseglio-Polatera (1992) illustrate how such information can be summarized and expressed. In this paper, we used data collected from published and unpublished reports (since 1978) to obtain information on the occurrence of Plecoptera and Ephemeroptera in a large range of lotic or lentic habitats of the Upper Rhône River and its floodplain in France. Information on habitat utilization then was linked to information on the species traits of these two insect orders.

Previous studies of the ecology of the Ephemeroptera or Plecoptera have emphasized only a few species traits, and often these have been considered independently. The egg stage, which is especially important because it is more resistant to the external environment than either the adult or nymphal stage (Brittain, 1990), has received particular attention. Other studies have examined fecundity and oviposition behaviours (reviewed in Humpesch & Elliott, 1984), parthenogenesis (e.g. Degrange, 1960; Hynes, 1976; Humpesch, 1980a; Brittain, 1982), hatching time (e.g. Humpesch, 1980b,c, 1982; Brittain, Lillehammer & Saltveit, 1984; Brittain & Lillehammer, 1987; Elliott,

1984, 1987a,b, 1988, 1991; Lillehammer *et al.*, 1989), diapause (e.g. Khoo, 1968; Bohle, 1972; Hynes, 1976; Zwick, 1981; Brittain, 1982), life cycles (Landa, 1968; Sowa, 1975; Macan, 1979), food (Kawecka, 1977; Kuusela, 1979), and dissemination potential (Söderström, 1981). Most of this autecological information is scattered throughout the literature.

Because of the complexity of the relationships among species traits or the relationship between species traits and habitat utilization, a multivariate approach is required for their analysis (cf. Statzner, Resh & Roux, 1994). Based on such an approach, the objective of this study is to examine the Ephemeroptera and Plecoptera of the Upper Rhône River in terms of: (i) the relationships among their species traits; (ii) the habitat utilization of species; (iii) the relationship between species traits and habitat utilization; and (iv) the trends of species traits and species richness in a framework of spatial–temporal habitat variability (see Cellot *et al.*, 1994), i.e. the river habitat templet developed by Townsend & Hildrew (1994).

Materials and Methods

Our study considers the Ephemeroptera and Plecoptera of two sections of the French Upper Rhône: Jons, a relatively unpolluted site close to Lyon, and Brégnier-Cordon, a site essentially undisturbed by river regulation until 1984 (cf. Cellot *et al.*, 1994).

Selection of species

The faunal list (Appendix 1) was obtained from several benthic surveys involving devices such as dredges (Berly, 1988), artificial substrates (Perrin, 1978), suction pumps or Surber nets (Gaschignard-Fossati, 1986), hand nets (Castella, 1987), or specific methods developed to sample submerged banks (Cogérino, 1989). In addition, imagines were collected with light traps (Usseglio-Polatera, 1985). Sampling in these and other studies of Ephemeroptera and Plecoptera at the two sections studied focused on spatial and/or temporal patterns and included quantitative, semi-quantitative, and qualitative approaches. Only taxa with reliable taxonomic determinations at the species level were used. Groups with difficult or unreliable species identification were eliminated, e.g. the Plecoptera genera *Nemoura, Amphinemura, Protonemura* (all Nemouridae), *Taeniopteryx* (Taeniopterygidae), and *Capnia* (Capniidae), and Ephemeroptera of the *Ecdyonurus helveticus* or *venosus* groups (except *Ecdyonurus ruffii*). In addition, species for which most species traits were unknown were also omitted. Therefore, fifty-five species, of which forty-one were species of Ephemeroptera belonging to nine families (mainly Baetidae, Heptageniidae, and Leptophlebiidae) and fourteen were species of Plecoptera representing five families, were selected

Table 1 Species traits and modalities (= categories, plus their numbers used as labels in the figures) of Plecoptera and Ephemeroptera used in this analysis. l, larvae; i, imagines

No.	Species trait	No.	Modality	No.	Species trait	No.	Modality
1	Potential size	1	≤5 mm	9	Dissemination	1	≤10 m
		2	>5–10 mm		potential (l)	2	>10–100 m
		3	>10–20 mm			3	>100–1000 m
		4	>20 mm			4	>1000 m
2	Potential no. of	1	≤1000	10	Dissemination	1	≤100 m
	descendants per	2	>1000–3000		potential (i)	2	>100–1000 m
	reproductive cycle*	3	>3000			3	>1000 m
3	Potential no.	1	<1	11	Attachment	1	Swimmers
	of reproductive	2	1		to soil or	2	Crawlers
	cycles per year	3	2		substrate (l)	3	Burrowers
		4	>2	12	Body	1	None (≤10°)
4	Adult longevity	1	≤1 day		flexibility (l)	2	Low (>10–45°)
		2	>1–10 days			3	High (>45°)
		3	>10–30 days	13	Body form (l)	1	Streamlined
		4	>30 days			2	Flattened
5	Reproductive	1	Single individual[†]			3	Cylindrical
	technique	2	Direct: male and female[†]	14	Diapause	1	No diapause
6	Sex ratio	1	<50%			2	Embryonic diapause
	(% of females)	2	50%			3	Larval diapause
		3	>50%	15	Feeding habits	1	Shredders[‡]
7	Reproductive	1	March		(l)	2	Scrapers
	period	2	April			3	Deposit feeders
		3	May	16	Food (l & i)	1	Detritus ≤1 mm (l)
		4	June			2	Detritus >1–10 mm (l)
		5	July			3	Detritus >10 mm (l)
		6	August			4	Living plants ≤1 mm (l)
		7	September			5	Living plants >1–10 mm (l)
		8	October			6	Living plants >10 mm (l)
		9	November			7	Living animals ≤1 mm (l)
		10	December			8	Living animals >1–10 mm (l)
8	Parental care	1	Isolated eggs			9	Living animals >10 mm (l)
		2	Eggs in vegetation			10	Living plants >1–10 mm (i)
		3	Gelatinous eggs			11	No feeding/assimilating (i)
		4	Cemented aquatic eggs	17	Respiration	1	Aerial (spiracle)
		5	Ovoviviparity		(l & i)	2	Aquatic (gills)
						3	Aquatic (tegument)

* Fecundity.
[†] Parthenogenetic or sexual.
[‡] Includes shredding predators.

Species traits

from the approximately seventy species recorded for these two orders at the two sites. In considering species richness in the framework of spatial–temporal habitat variability, all species with reliable determination were used.

Information on species traits was gathered from a very large and scattered bibliography (almost 1200 references consulted). Of the eighteen species traits that had been selected for the study of all organisms (Dolédec & Statzner, 1994), five ('potential number of reproductive cycles per individual', 'tolerance to

variation in humidity', 'resistant life stages', 'potential for regeneration of an individual', and 'variability of habitat use') were removed, and four new species traits that better synthesized nutrition or reproduction strategies were added: 'adult longevity' (variable 4 in Table 1), 'sex ratio' expressed as the percentage of females (variable 6), presence of a dormancy period ('diapause' or quiescence; variable 14), and 'feeding habits' (variable 15). Moreover, we used the trait 'dissemination potential' in place of 'distance travelled with or against current'. For this trait, we distinguished between the larval and the adult stage (variables 9 and 10).

The availability of information on these species traits varied considerably among species. Table 2 gives an example for a

Table 2 Number of references that contained relevant information on the seventeen species traits for a well-documented species [*Baetis rhodani* (Pictet)] and a poorly documented species (*Baetis pentaphlebodes* Ujhelyi) of Ephemeroptera. l, larvae; i, imagines. See Table 1 for full labels of species traits

	Species trait	B. rhodani	B. pentaphlebodes
1	Size	14	4
2	Descendants per cycle	8	1
3	Cycles per year	34	4
4	Adult longevity	1	1
5	Repro. technique	1	?*
6	Sex ratio	4	1
7	Repro. period	21	4
8	Parental care	10	1
9	Dissemination (l)	11	?*
10	Dissemination (i)	12	2
11	Attachment	3	6
12	Body flexibility	3	1
13	Body form	3	1
14	Diapause	7	?*
15	Feeding habits	4	1
16	Food	11	1
17	Respiration	1	1

* For these poorly documented traits, we used information from the same group (*buceratus*) or the same genus.

well-documented species and a poorly documented one. For the latter, information on closely related species was substituted when possible.

The affinity between species of Ephemeroptera and Plecoptera and their species traits was described using 'fuzzy coding' (Chevenet, Dolédec & Chessel, 1994) in the following way: 0, the species had no link with a modality (= category); 1, the species had weak links with a modality; 2, the species had moderately strong links to a modality; and 3, the species was strongly related to a modality. When the trait concerned different stages of the life cycle (egg, larva, subimago and/or imago), we considered the relative duration of each stage in defining the score of a modality (cf. Tachet, Usseglio-Polatera & Roux, 1994). The resulting information consisted of an array with fifty-five species × seventeen species traits (Appendix 2).

Habitat utilization

The twenty-two habitat types of the Upper Rhône River considered in this issue have been defined on the basis of geomorphological considerations and on differences in biological characteristics (Bravard, Amoros & Pautou, 1986; Cellot *et al.*, 1994). However, the available information on the distribution of Ephemeroptera and Plecoptera only allowed analysis of thirteen of these habitat types (see Fig. 3).

In coding for the different habitats of Jons and Brégnier-Cordon, we made a distinction between occurrence of the aquatic (egg, larva) and terrestrial stages (subimago and/or imago). For the aquatic stages, we coded the relative (intra-specific) abundance of larvae in the different habitats. For the adult stages, we considered the dispersion potential of the species. As with the species traits, we considered the relative duration of each stage and all information was structured using 'fuzzy coding'.

Therefore, habitat information consisted of distribution profiles for each of fifty-five species in a set of thirteen habitat types. This information was obtained from previously cited and other published or unpublished studies of the Ephemeroptera and the Plecoptera of the Upper Rhône.

Data analysis

A multivariate approach was used to examine the relationships among species traits, the habitat utilization of the species, and the relationship between species traits and habitat utilization. The species trait and habitat utilization arrays were analysed using methods described by Chevenet *et al.* (1994) and Dolédec & Chessel (1994). Thus, a fifty-five species by seventeen species trait array and a fifty-five species by thirteen habitat utilization array were processed by correspondence analysis; then these arrays were matched by co-inertia analysis (i.e. the simultaneous ordination of the two arrays), which demonstrates the common structure (= co-structure or relationship) of the two tables and results in a common numeric coding of species according to species traits and habitat types.

To test the predictions of the river habitat templet (Townsend & Hildrew, 1994) and the patch dynamics concept (Townsend, 1989), the different habitat types of the Upper Rhône River and its alluvial floodplain were positioned in a framework of spatial and temporal variability (Cellot *et al.*, 1994). The families and species of Plecoptera and Ephemeroptera were placed in this framework of spatial and temporal variability according to the habitats colonized by them. Species traits also were positioned in the same framework according to species representing them. A comparison of the two series of graphs enables examination of predictions on patterns of species traits in the framework of spatial and temporal variability. The number of species occurring in each habitat type was then examined in the same framework.

Results

Relationships among species traits

The eigenvalue diagram (Fig. 1a) that results from the correspondence analysis of the species trait array clearly indicates the importance of the F1 axis, which explains 23.5% of the total inertia; the F2 axis explained only 11.4% of the total inertia. Thus, the F1 axis may be regarded as the numerical coding that best summarizes the relationships among species traits (Fig. 1b).

The species traits that are best explained by the first two factorial axes are indicated by elevated correlation ratio values (Fig. 1b). The species traits
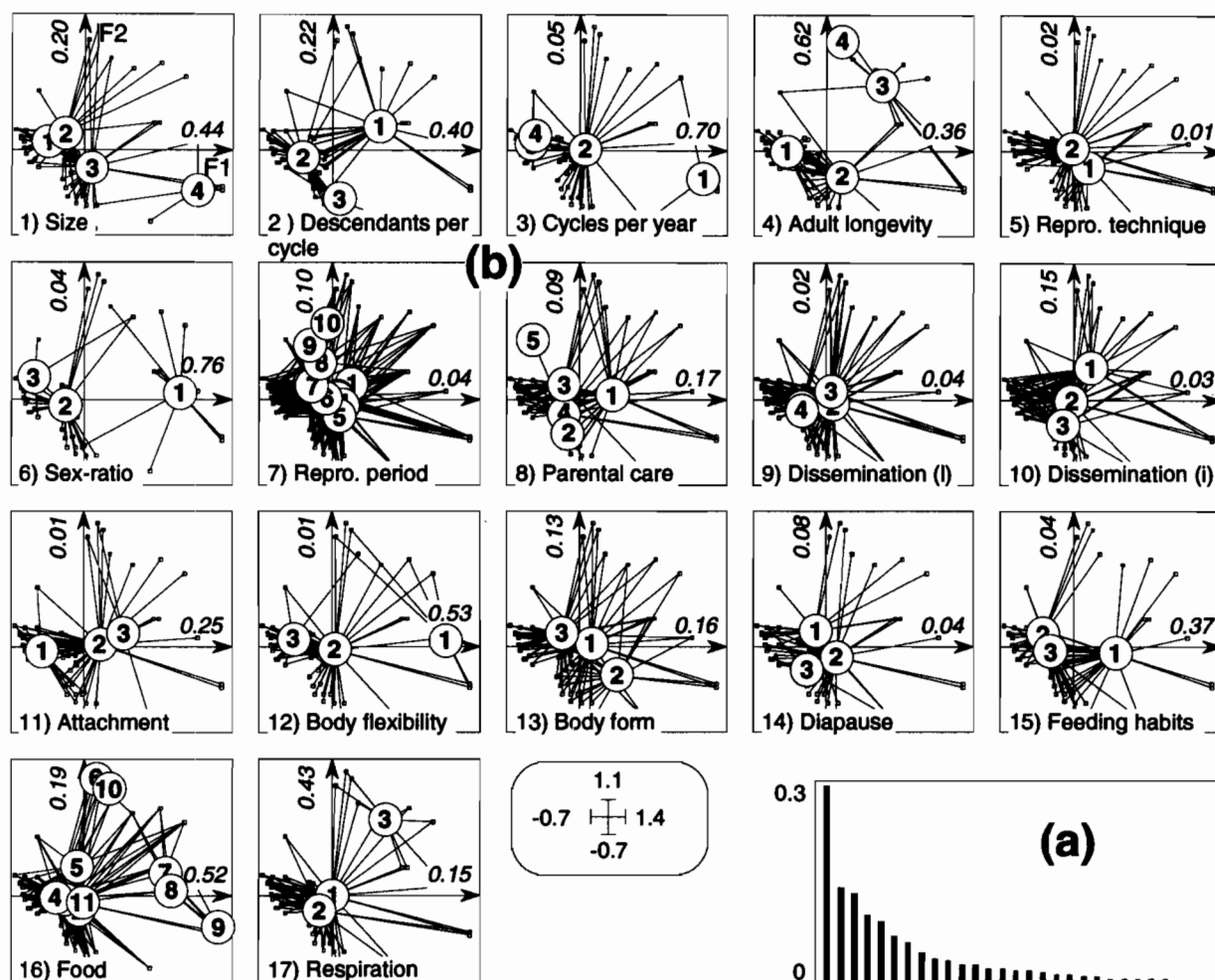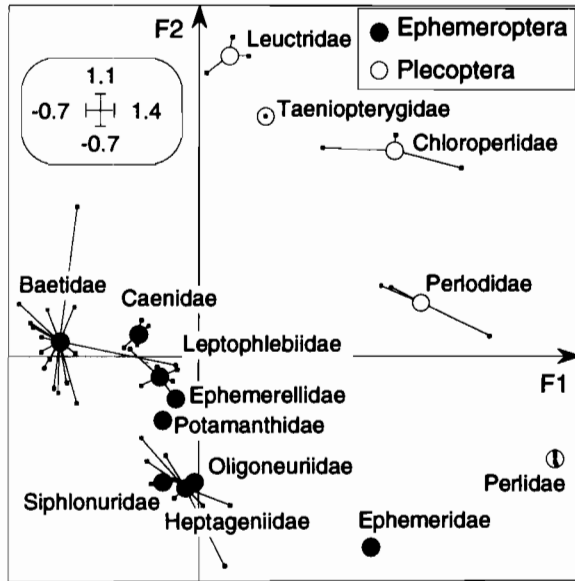
Fig. 1 Ordination of species traits by correspondence analysis. (a) Histogram of eigenvalues. (b) Distribution of modalities (the numbers in circles) of seventeen species traits on the F1 × F2 plane, with correlation ratios for each species trait indicated on the axes (see Table 1 for full labels of species traits and trait modalities; for traits that exhibit a gradient, modality no. 1 is at the lowest, earliest, or least intense end of the gradient). Small squares represent the species. Each modality is positioned at the weighted average of species representing this modality. Lines link species to their modalities.

having the highest correlation ratios on axis F1 correspond to reproduction or life cycle [i.e. 'number of descendants per reproductive cycle' (variable 2 in Fig. 1b), 'number of reproductive cycles per year (variable 3), 'adult longevity' (variable 4), 'sex ratio' (variable 6)], behavioural or physiological [i.e. 'feeding habits' (variable 15), 'food' (variable 16)] and morphological [i.e. 'potential size' (variable 1), 'body flexibility' (variable 12)] characteristics (correlation ratios times 100 = 36–76% of explained variance). Two species traits are of special interest along axis F2: 'adult longevity' (variable 4) and 'respiration' (variable 17), both of which are widely scattered along this axis (Fig. 1b).

By comparing the position of modalities and families in Figs 1b and 2, it is apparent that two faunistic groups are in opposition on axis F1 in terms of their species traits. At the negative side are species with a small potential size (variable 1), a high number of descendants per cycle (variable 2) and several cycles per year (variable 3). Their imaginal stages are short lived (variable 4) and females predominate (variable 6). Their larvae are flexible (variable 12), mainly swimmers (variable 11), and scrapers or deposit feeders (variable 15). Most species of Baetidae, Caenidae, and Leptophlebiidae (Ephemeroptera) belong to this group.

At the positive side of the F1 axis (Figs 1b and 2)

Fig. 2 Ordination of species traits by correspondence analysis. Distribution of families (circles) of Ephemeroptera and Plecoptera on the F1 × F2 plane that are positioned at the weighted average of their species (small squares). Lines link species to their family.
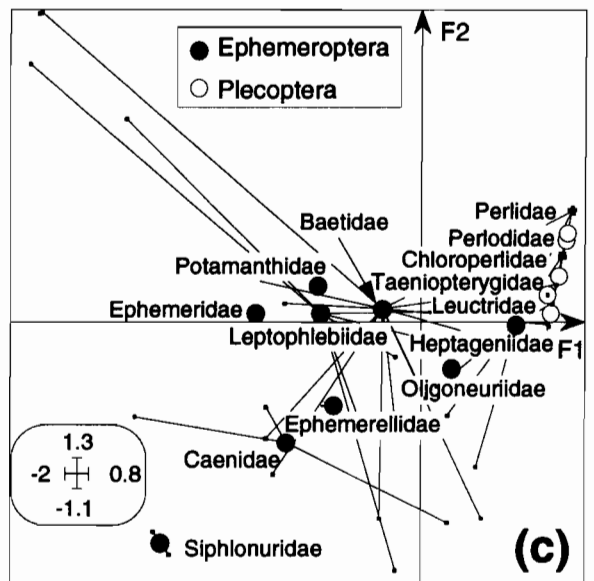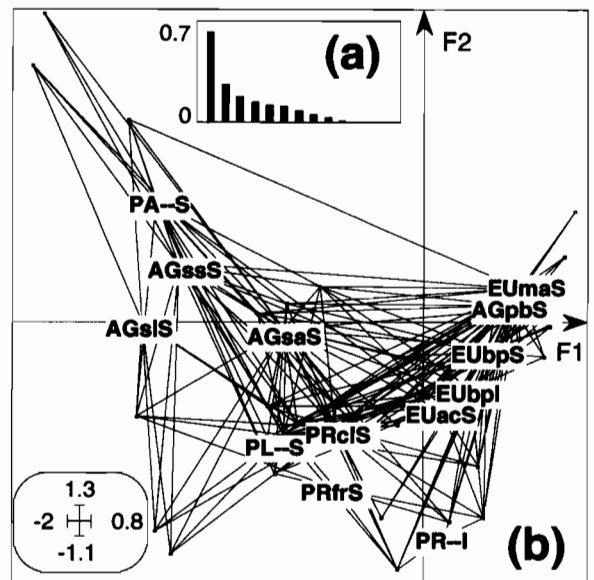
are semi- or univoltine species with a large potential size and a low fecundity. They are characterized by an intermediate adult longevity and usually a predominance of males. Their larvae are shredders, and more often carnivorous than those described above. Species of Perlidae and Perlodidae (Plecoptera) belong to this group.

In the F2 direction, larvae without gills (some species of Plecoptera) are distinctly separated from

Fig. 3 Ordination of habitat types by correspondence analysis. (a) Histogram of eigenvalues. (b) Distribution of habitat types on the F1 × F2 plane. Small squares represent the species. Each five character identifier of the habitat types is positioned at the weighted average of species found in that habitat type. Lines link species to habitat types. Habitat type identifiers (for details see Cellot *et al.*, 1994); XX——: AG, aggrading; EU, eupotamon (various channel types); PA, paleopotamon (oxbow lake, former meander or anastomosed channel); PL, plesiopotamon (oxbow lake, former braided channel); PR, parapotamon (backwater in permanent connection with the main channel, former side arm of a braided channel); —xx-: —, no specification; ac, artificial channel; bp, bypassed section; cl, close to the main channel; fr, far from the main channel; ma, meander or anastomosed or main channel; pb, pebble; sa, sand; si, silt; ss, sand–silt; ——X: I, interstitial; S, superficial. (c) Distribution of families (circles) of Ephemeroptera and Plecoptera on the F1 × F2 plane (see Fig. 2 for further details).
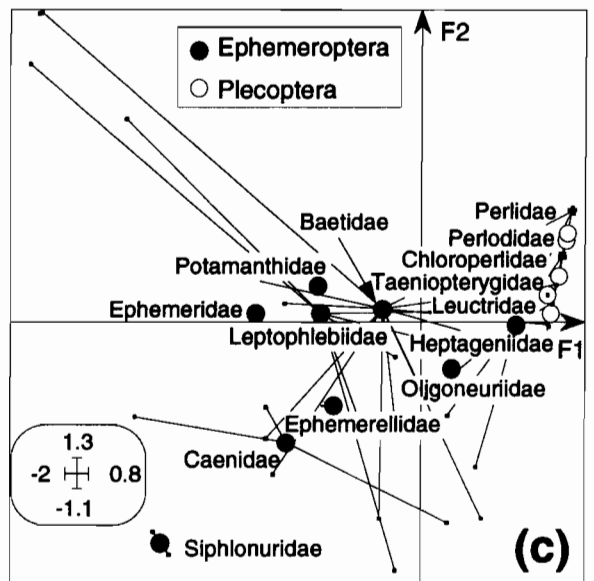
larvae with branchial respiration (Figs 1b and 2). In the same way, species with a potentially long adult life span (most of the Plecoptera) are opposite species with a short adult life span (most of the Ephemeroptera).

Habitat utilization

The eigenvalues (Fig. 3a) of the correspondence analysis of the habitat utilization array indicate that the F1 axis (36.7% of total inertia explained) is distinctly more important than the F2 axis (15.8% of total inertia explained). The F1 scores clearly dem-

onstrate a transverse gradient, with the different habitat types organized along the F1 axis based on the intensity of their relation with the main channel; the gradient occurs from the active channel (F1 > 0) to the paleopotamon that is completely isolated from the main channel (Fig. 3b). The 'aggrading' habitats that are only temporarily colonized by the adult stages of the Ephemeroptera and Plecoptera are positioned on the factorial map according to their neighbouring aquatic habitats. Axis F2 partly expresses a vertical gradient, with the scores of the interstitial habitats (at 50 cm below the substrate surface) always being lower than the scores of the corresponding superficial habitats (Fig. 3b).

Fig. 3c indicates a strong association of Plecoptera and Heptageniidae species with the different main channel (eupotamic) habitats. In contrast, the Baetidae, Caenidae, and Leptophlebiidae show a broad distribution across a variety of habitats.

Relationship between species traits and habitat utilization

To examine the significance of the correlation between the two sets of projected coordinates of species resulting from the co-inertia analysis, we used a permutation test (Dolédec & Chessel, 1994). This test compares the observed R^2 value for a co-inertia axis to the distribution of R^2 values obtained with 200 co-inertia analyses using random matching of the two data files, which were produced by randomly permutating the rows. The test for the co-inertia axis F1 is significant ($P < 0.005$). In contrast, the co-inertia axis F2 is not significant ($P = 0.36$). The eigenvalue diagram emphasizes this difference between the two axes (Fig. 4a); however, we have retained axis F2 for comparison with the standard analysis of each array (species traits or habitat utilization).

The projection of the axes of the separate analyses on the co-inertia axes indicates that the co-inertia axes F1 adequately expresses the inertia axes F1 of these separated analysis (Fig. 4b). The co-inertia axis F2 is a mixture of the inertia axes F2 and F3 for the habitat utilization and of the inertia axes F2 to F5 for the species traits.

Comparing the positions of habitat types (Fig. 4c), trait modalities (Fig. 5), and species vectors (Fig. 6) on the F1 × F2 plane summarizes the results of the co-inertia analysis. The thirteen habitat types are
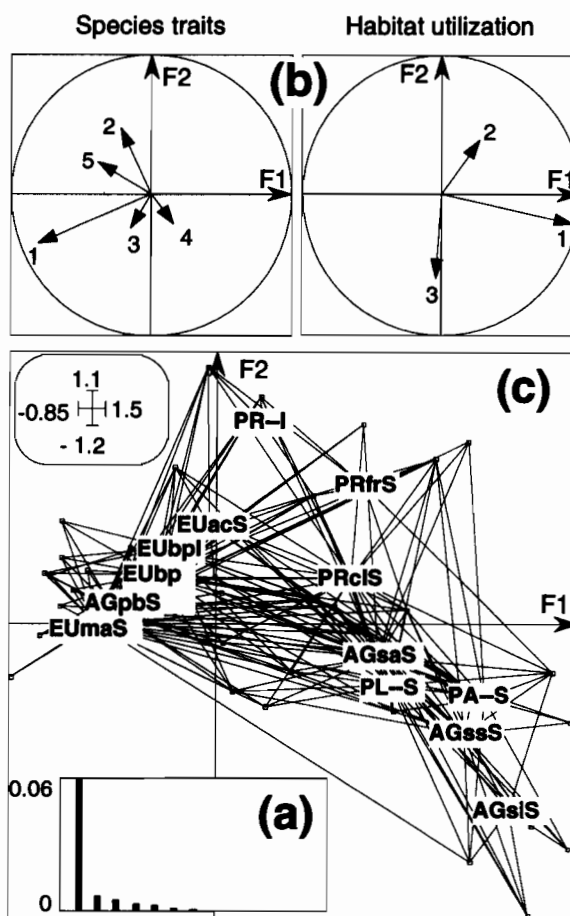
Fig. 4 Co-structure between species traits and habitat utilization by co-inertia analysis. (a) Histogram of eigenvalues. (b) Relationships between separate analyses and co-inertia analysis. Each arrow represents an axis number of the previous correspondence analysis (species traits or habitat utilization) that are projected on to the co-inertia axes (F1 and F2). (c) Ordination of habitat types (located by the five character identifier) on the F1 × F2 plane with species (small squares) positioned according to their species traits (see Fig. 3 for further details).

distributed along a transverse gradient, from the main channel to the oxbow lakes, on axis F1 (Fig. 4c). The main channel (EUmaS), the bypassed sections (EUbpS), and the artificial channel (EUacS) at the negative side are opposite the parapotamons (PRfrS, PRclS), the plesiopotamon (PL−S), and the paleopotamon (PA−S). Again, the aggrading habitats are ordinated close to the position of their neighbouring aquatic habitat types. This transverse gradient more or less corresponds to: (i) a decreasing gradient of 'size' [variable 1 in Fig. 5, with a large potential size for the dominant eupotamic species, which are

mainly Plecoptera (see Fig. 6) and a small potential size for species of lenitic habitats]; (ii) an increasing gradient of fecundity (variable 2) and 'number of reproductive cycles per year' (variable 3); (iii) a decreasing 'adult longevity' (variable 4) but an increasing percentage of females (variable 6); and (iv) a gradual modification of morphological ['body flexibility' (variable 12) and 'body form' (variable 13)] and behavioural ['dissemination potential' (variable 9)] species traits. Eupotamic larvae are more often streamlined, and are crawlers with a low body flexibility; their mobility, mainly linked with their ability to drift, is high. In contrast, species occurring in former main channel habitats (cf. Figs 4c and 5) are

more often cylindrical in shape, swimmers (i.e. actively moving), and flexible (i.e. they move by body undulations); their mobility is low. Moreover, there is a diversification of egg-laying modalities (variable 8); the aquatic, cemented eggs are the only efficient technique usable in lotic habitats. Finally, there is a gradual evolution of 'feeding habits' (variable 15) and ingested 'food' (variable 16): shredders and carnivorous species are dominant in eupotamic habitats; scrapers, linked with plant material, are dominant in parapotamons and the plesiopotamon; and deposit feeders, feeding on organic detritus, are dominant in the paleopotamon (Figs 4c and 5).

On the factorial map of the co-inertia analysis,
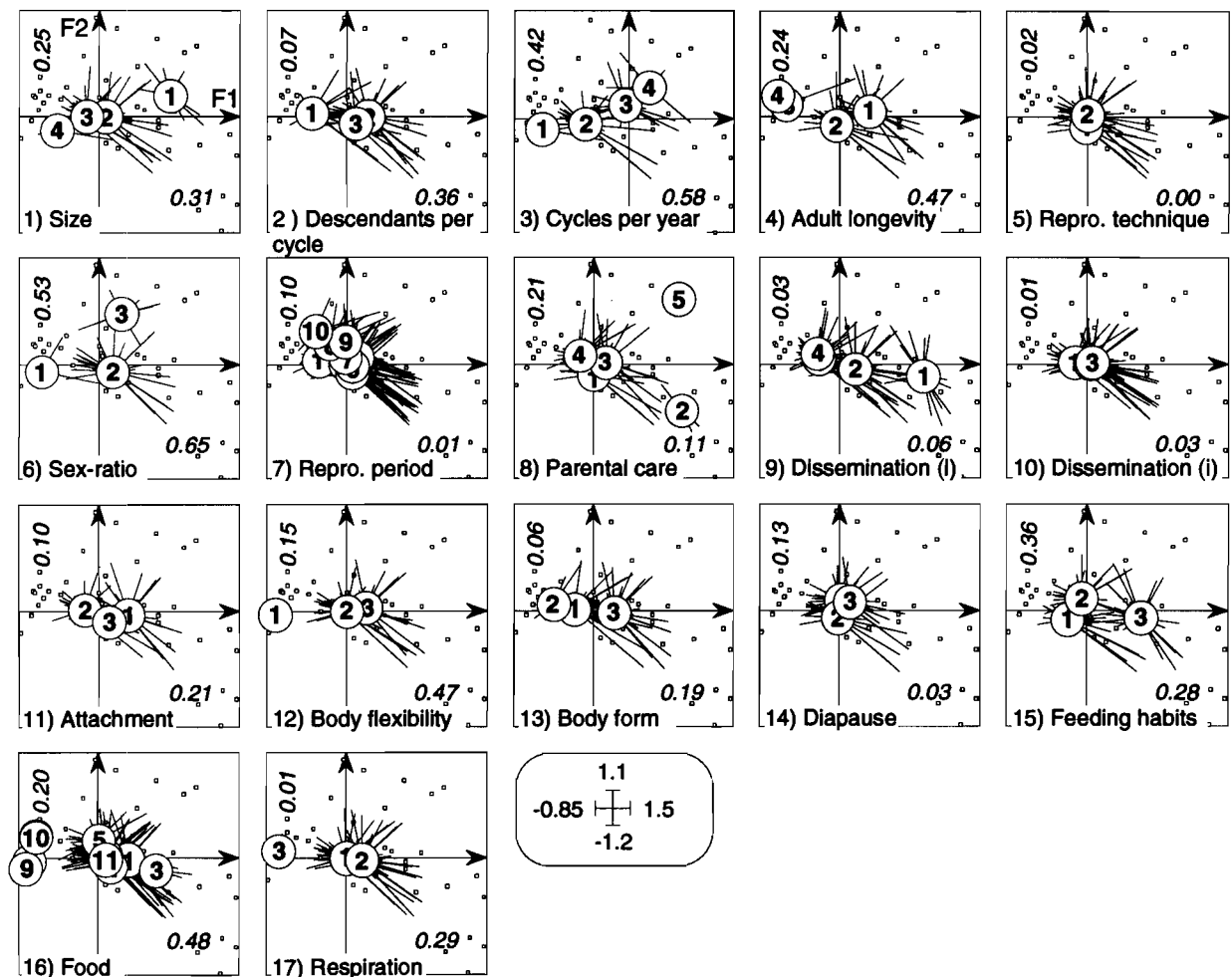
Fig. 5   Co-structure between species traits and habitat utilization to co-inertia analysis. Ordination of species traits on the F1 × F2 plane with species (small squares) positioned according to their habitat utilization (see Fig. 1 for further details). In this figure, lines linking species to their modalities are only 50% of their total length for readability; lines are omitted if a species contributed less than 1% to the modality distribution.
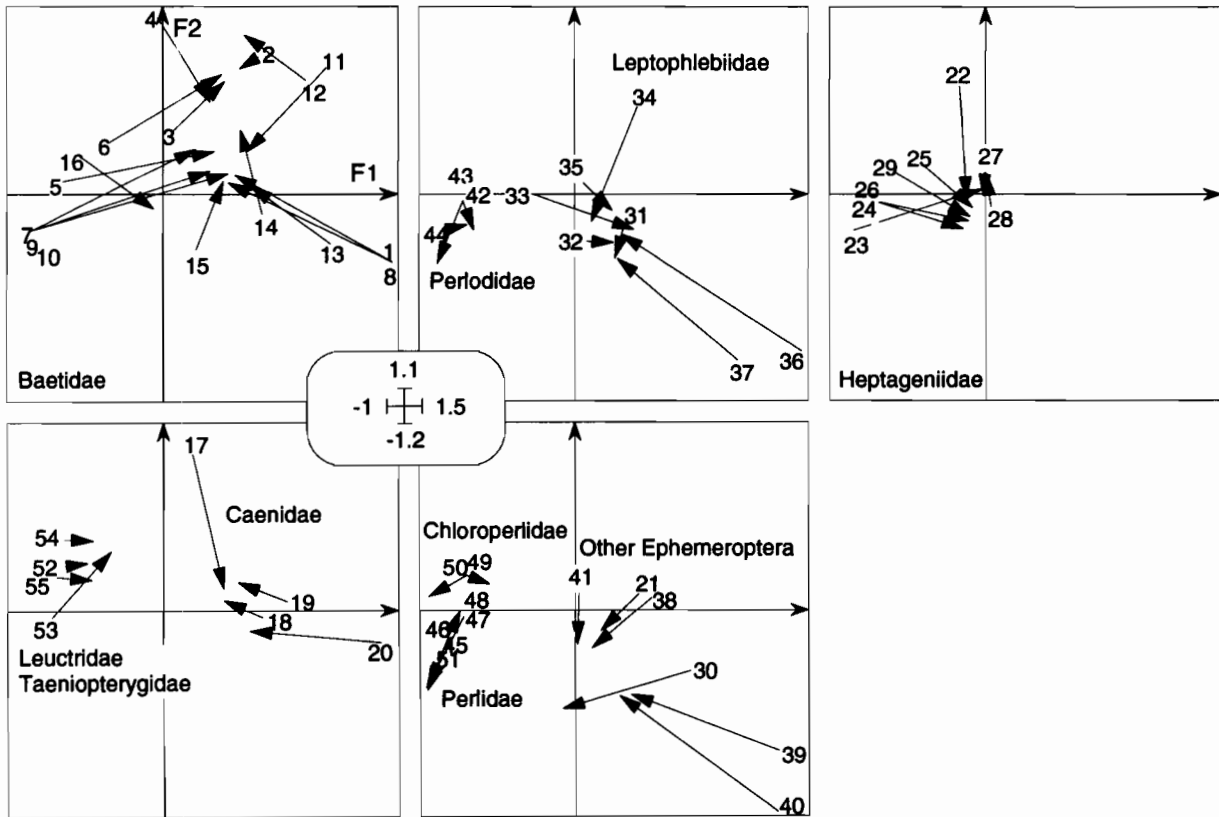
Fig. 6 Comparison of species positions on the two F1 × F2 planes by co-inertia analysis (see Fig. 4 for eigenvalues). Each species (see Appendix 1 for species numbers) is defined by an arrow. The beginning of the arrow marks the position according to the habitat utilization of a species and the end of the arrow marks its position according to the species traits.

each species is defined as a vector plotted between its position according to habitat utilization (the beginning of the arrow) and its position according to species traits (the end of the arrow; Fig. 6). The high number of long arrows parallel to the F1 axis ($P < 0.005$; see above) indicates that there is little superposition of the species traits of Ephemeroptera and their habitat utilization. Most of the species in the different families of Ephemeroptera have similar species traits (the ends of the arrows are close together) but very different spatial distributions (Fig. 6); the Baetidae, which display a great diversity of species traits (and spatial distributions) are an exception. In contrast, the Plecoptera exhibit a strong co-structure between species traits and habitat utilization, i.e. the arrows are all rather short (Fig. 6).

Species traits, species richness, and spatial−temporal variability

In terms of the arrangement of the habitat types in the templet scaled by Cellot *et al.* (1994), the eupotamic (with the exception of the superficial bypassed sections, EUbpS) and interstitial habitats are habitat types with the lowest spatial and temporal variability (Fig. 7a). Other aquatic superficial habitats (EUbpS, PA−S) exhibit low to intermediate spatial variability and intermediate temporal variability. The superficial habitats of a third group (PRfrS, PRclS, PL−S) display intermediate to high spatial variability, while the temporal variability of habitats in this group is intermediate. Aggrading habitats (AGsaS, AGssS, AGpbS, AGsiS) vary to some extent and this occurs also over the temporal axis (Fig. 7a).

The distribution of species and families in the spatial−temporal framework of habitat variability is

Fig. 7 Habitats and families of Ephemeroptera and Plecoptera in the templet of spatial—temporal habitat variability. (a) Position of habitat types in the templet of spatial—te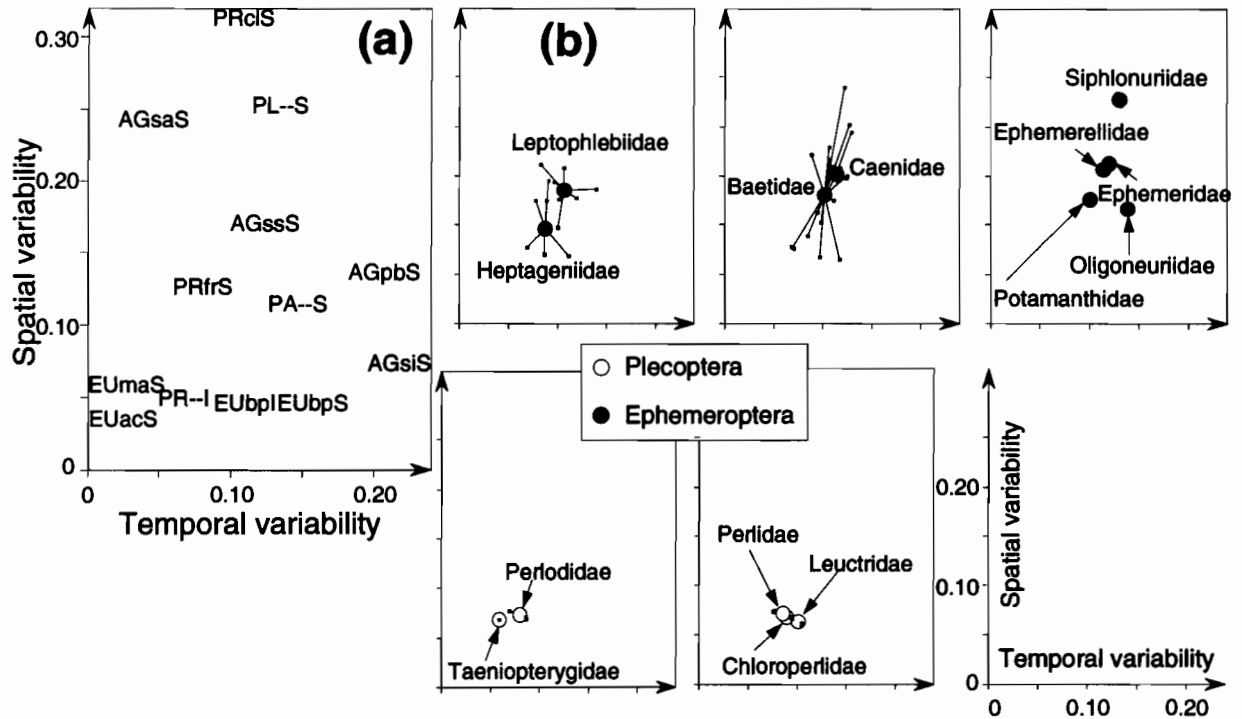mporal variability (see Fig. 3 for habitat identifiers). The templet axes indicate cumulated variability of factorial scores for eight environmental variables (cf. Cellot *et al.*, 1994). (b) Distribution of species (small squares), and families (circles), which are at the weighted average of their species) in the same templet.

illustrated in Fig. 7b. Ephemeroptera and Plecoptera can be divided into three groups, mainly on the basis of the spatial variability of their habitat utilization. Group 1 corresponds to species located where the spatial variability is the lowest. Species of Taeniopterygidae, Perlodidae, Perlidae, Chloroperlidae, and Leuctridae belong to this first group. Group 2 consists of species colonizing a large variety of habitats with very different spatial variabilities. Most of the species of the Baetidae and, to some degree, species of Caenidae, Leptophlebiidae, and Heptageniidae belong to this second group. Group 3 is represented by species located in an area where the spatial variability is high. The Siphlonuriidae belong to this third group.

A permutation test (cf. Chevenet *et al.*, 1994) indicates that trends in species traits are significant ($P < 0.005$) along the axes of spatial and temporal variability. In analysing these trends of traits (Fig. 8), it is apparent that species with characteristics such as large body size (variable 1 in Fig. 8), low fecundities (few descendants and fewer females, variables 2 and

6) and long individual life spans (variables 3 and 4) tend to occur in temporally more stable environments. Their larvae are adapted to high current speeds (i.e. they are streamlined or flattened crawlers, variables 11 and 13) that are very mobile (variable 9), and they are specialized in their use of food (animals, variable 16). In contrast, small species occurring in habitats of elevated temporal variability compensate for this habitat instability by having high fecundities (more females, many descendants) and a shortened life cycle (short imaginal life span, polyvoltinism). Their larvae, with a low dissemination potential (imagines are predominant in dispersal), display little specialization in their use of food (i.e. they are mainly deposit feeders of detritus).

Plotting species richness into the habitat templet reveals no apparent trends in species richness along the spatial and temporal axis (Fig. 9). Highest species richness is observed in the main channel (used by aquatic stages) and in its neighbouring aggrading habitat (AGpbS; used by imaginal or subimaginal stages).
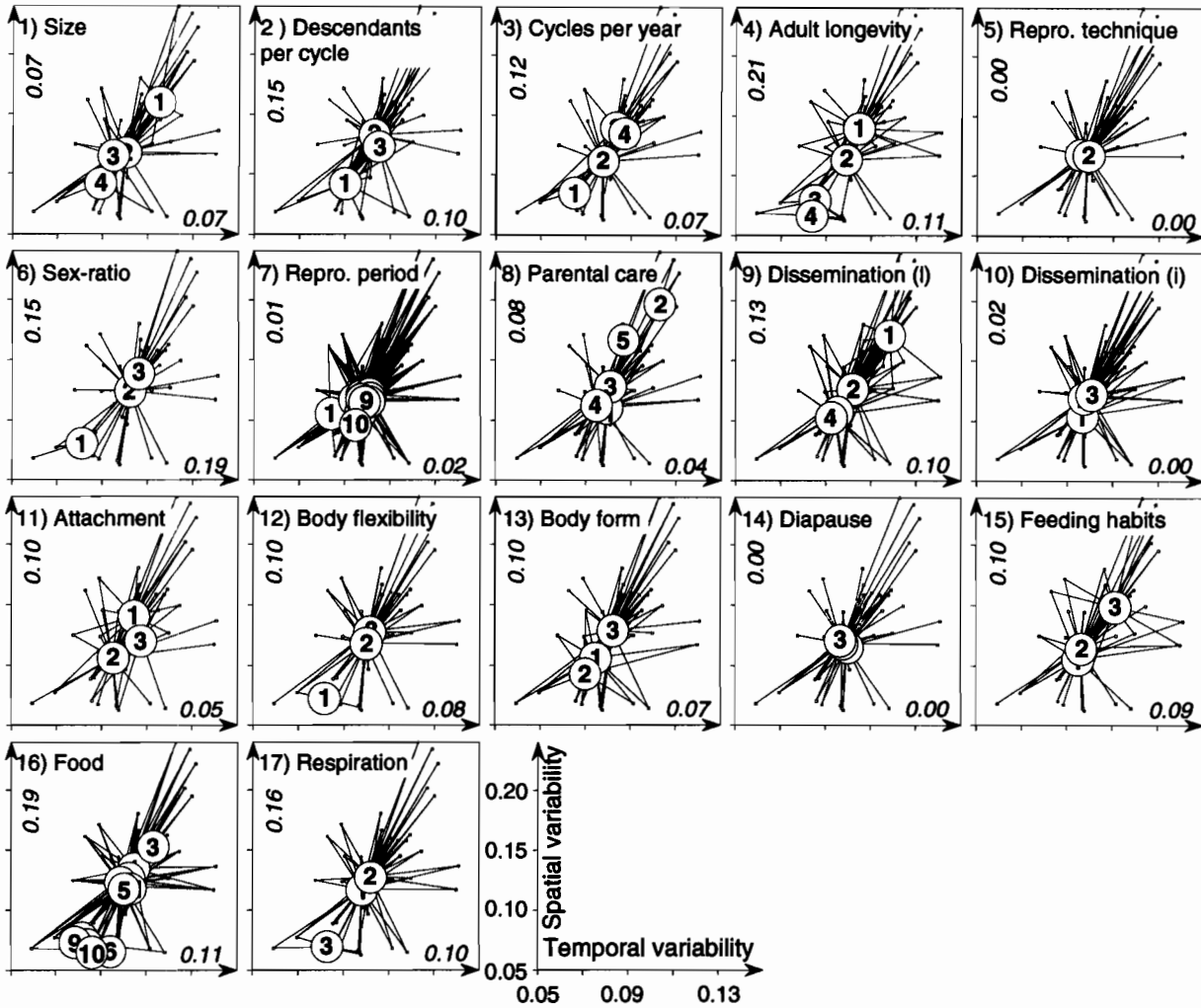
Fig. 8 Species traits in the templet of spatial−temporal habitat variability. Species (small squares) are positioned at the weighted average of their habitat utilization and each modality (the number in a circle) is positioned at the weighted average of species representing that modality (see Fig. 1 for further details).

Discussion

Relationships among species traits

The location of species within each systematic group relative to the location of species in other systematic groups (orders or families) is distinct (Fig. 2). Plecoptera species are totally separated from Ephemeroptera species by the distribution of modalities in species traits such as 'adult longevity' (variable 4 in Fig. 1b). Most Plecoptera are also distinguished from Ephemeroptera by a mixture of characteristics such as 'number of descendants per reproductive cycle' (variable 2), 'sex ratio' (variable 6), 'body flexibility' (variable 12), 'food' (variable 16), and/or 'respiration' (variable 17).

Even though the $r-K$ concept has been criticized for being too deterministic (e.g. Stearns, 1977; Ladle & Ladle, 1992; and many others), some of its general trends appear to apply to the two orders of insects examined in this study. The major structure emphasized by the first axis corresponds to a $r-K$ gradient from the Ephemeroptera families Baetidae and Caenidae towards the Plecoptera families Perlodidae and Perlidae because the separation among species is at least partly based on reproductive traits (e.g. variables 2 and 3). The 'number of reproductive cycles per year' and the 'sex ratio', expressed as the percentage of females, decrease and the 'potential size' increases along this gradient, corresponding to the patterns predicted by the $r-K$ concept. In addition,
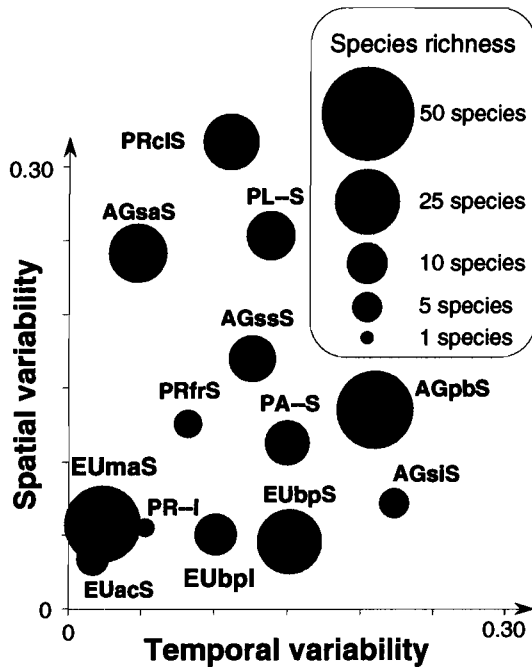
Fig. 9 Species richness of Ephemeroptera and Plecoptera in the templet of spatial–temporal habitat variability. The size of the circles is proportional to the species richness in a habitat (see Fig. 3 for habitat identifiers).

the 'number of descendants per reproductive cycle' is lower (though not clearly) at the K side of the gradient (Fig. 1b). Furthermore, the observed gradient (along the second axis) also corresponds to a contrast between: (i) species that in general exhibit a short adult life, have a high number of descendants per reproductive cycle, and have larvae with branchial respiration, which should be more effective in new or disturbed habitats (at the negative side of the F2 axis); and (ii) long-lived species, having a low number of descendants per reproductive cycle, and having larvae without gills (at the positive side of the F2 axis; Fig. 1b).

Habitat utilization

Both a vertical and especially a transverse gradient are demonstrated by the ordination of habitats (Fig. 3b). The applicability of the river typology initially developed on geomorphological and biological considerations by Bravard *et al.* (1986) is thus confirmed. Plecoptera and Heptageniidae species are dominant in the different main channel habitats. Caenidae, Siphlonuridae, and Ephemerellidae species occur

mainly in the parapotamon and plesiopotamon. The Baetidae and Leptophlebiidae species are present in most types of habitats (Fig. 3c).

Relationship between species traits and habitat utilization

There is a general gradient in species traits and in the habitats in which these traits occur from lotic to lentic environments (for both interstitial and superficial habitats; Figs 4c and 5). For the Ephemeroptera (and especially for the Heptageniidae and Leptophlebiidae), the ordination of species displays a higher variability in the position of species according to the habitat utilization than in the position of species according to their species traits (Fig. 6), indicating that species can use a variety of habitat types despite having quite similar species traits. In contrast, the Plecoptera display a strong homogeneity in their species traits and use fewer, lotic habitat types.

The strong organization of species trait modalities and their gradual shift from the main channel towards the oxbow lakes demonstrate: (i) the relevance of traits such as 'potential size' (variable 1 in Fig. 5), 'number of reproductive cycles per year' (variable 3), 'adult longevity' (variable 4), 'sex ratio' (variable 6), 'body flexibility' (variable 12), 'feeding habits' (variable 15), 'food' (variable 16), and/or 'respiration' (variable 17) for the habitat utilization; and (ii) clear limitations in the habitat utilization for all Plecoptera and some Ephemeroptera species (Fig. 6)

Species traits and spatial–temporal habitat variability

A fundamental goal of ecology is to synthesize ecological information and then to predict how species, populations, and communities respond to environmental changes (Power *et al.*, 1988). Species react to the fluctuating environment of streams and rivers by appropriate biological and ecological responses that depend on the constraints on their morphological, physiological, or behavioural characteristics that arise from their phylogenetic history (cf. Hodgson & Mackey, 1984; Southwood, 1988; Townsend & Hildrew, 1994). Processes that structure communities in lotic environments occur on different spatial and temporal scales. Temporal variability is assumed to be governed essentially by the frequency and

the magnitude of disturbances (Resh *et al.*, 1988; Townsend & Hildrew, 1994). According to the permutation test, temporal variability is of significant importance in structuring benthic assemblages of Ephemeroptera and Plecoptera in the habitats of the Upper Rhône. Habitats with low spatial and temporal variability correspond to two superficial types of the main channel (Fig. 7a). According to predictions about species traits in the river habitat templet of Townsend & Hildrew (1994), this relative stability enables colonization by species that exhibit a long larval life; the larval stage is of major importance in the dissemination of species (Fig. 8). These main channel habitats are assumed to be uncommonly (because of low temporal variability and frequency of disturbances) but severely (because of low spatial variability, corresponding to few refugia; cf. Townsend & Hildrew, 1994) disturbed by unpredictable events such as spates. Species must 'invest' in morphological and behavioural adaptations to 'hydraulic stress' (cf. Statzner, Gore & Resh, 1988), and development and survivorship of a species in such an adverse environment often requires each individual to have a greater investment in somatic development (Southwood, 1988). As a result, the observed size of species tends to be larger (Fig. 8). However, the heavier metabolic cost does not allow a large biomass allocation to reproduction (cf. Harper & Ogden, 1970; Wagner, 1981; Willows, 1987). In the spatial and temporal variability templet, we actually find only species with a low fecundity and a reduced number of cycles per year in the bottom left of the templet (Fig. 8), which supports the above views.

High larval mobility of species occurring at low spatial–temporal variability increases the effectiveness with which individuals actively or passively reach available refugia. Moreover, species re-establishment will depend on the proportion of the population that can move into refugia (Williams, 1984; Stanford & Ward, 1988; Townsend, 1989). High mobility also will allow individuals to avoid competition within a patch. In more constant habitats, the stability of potential resources facilitates the development of nutritional strategies (e.g. scrapers) that are specialized in using a particular food (e.g. organic microdetritus and/or microflora). This specialization must be an efficient adaptive solution in food harvesting under harsh abiotic conditions. However, competition becomes prominent under less

harsh environmental conditions, e.g. during periods of low discharge (Hemphill & Cooper, 1983; McAuliffe, 1984; Resh *et al.*, 1988). During these periods, organisms may be in competition with other species that are not as well adapted to harsh physical conditions. A negative correlation is often expected between adversity tolerance and competitive ability (Wilson & Keddy, 1986; Southwood, 1988; Townsend & Hildrew, 1994). Indeed, species that are typical of the most stable eupotamic environments (mainly Plecoptera) are often excluded from other habitat types (Fig. 7).

In the Rhône River floodplain, aquatic habitats with a high temporal variability correspond to plesiopotamons, paleopotamons, or temporary environments, and the bypassed sections of the main channel (Fig. 7a). Concepts of stability in running water ecosystems suggest that biological resilience in streams following disturbance is directly linked to the response of *r*-selected taxa (Webster *et al.*, 1983) that are capable of producing multiple generations per year as an adaptation to frequent perturbations. We found that species inhabiting the temporally variable habitats tend to have short life cycles (Fig. 8). The shortening of the larval stage is linked with characteristics such as small body size, and consequently larval development may be fulfilled during the short favourable periods.

Trends of species traits were significantly related to both the spatial and the temporal variability of the river habitat templet of Townsend & Hildrew (1994). However, testing their predictions was difficult because modalities of many variables were distributed along a diagonal from low to high spatial and temporal variability in the templet (Fig. 8), while their predictions were along a diagonal from low temporal/high spatial variability (habitat templet area A) to high temporal/low spatial variability (habitat templet area B; see Fig. 4 in Townsend & Hildrew, 1994). Consequently, each variability axis was considered separately.

Considering only temporal variability, which increases from habitat templet area A to B, the match between predictions and observations varied among the species traits (Table 3). Observed trends in the traits 'minimum age at reproduction' (derived from variables 3 and 4 in Fig. 8) and 'potential longevity' (also derived from variables 3 and 4) corresponded well to the predicted trends (Table 3). Four other

Table 3 Trends in species traits predicted in areas A and B of the river habitat templet (Townsend & Hildrew, 1994) and trends observed for the Ephemeroptera and Plecoptera in the Upper Rhône (focusing on traits for which predictions were available and on temporal variability, which increases from A to B). l, larvae; i, imagines. See Table 1 for full labels of species traits (trait numbers are added in parentheses)

Species trait	Habitat templet area A		Habitat templet area B	
	Predicted	Observed	Predicted	Observed
Size	Large–small	Large	Small	Small
Descendants per cycle (2)	Few–many	Few	Many	Many
Cycles per year (3)	<1–several	<1	Several	Several
Minimum age at reproduction*	Old–young	Old–young	Young	Young
Longevity (l & i)*	Long–short	Long–short	Short	Short
Reproductive technique (7)	Diverse	Diverse	Single individual	Diverse
Parental care (8)	Present–absent	Present–absent	Absent	Present–absent
Dissemination (l) (9)	Immobile–mobile	Relatively mobile	Mobile	Relatively immobile
Attachment (11)	None–firm	Firm	Firm	None–firm
Body flexibility (12)	Inflexible–flexible	Inflexible	Flexible	Flexible
Body form (13)	Diverse	Streamlined–flattened	Streamlined–flattened	Cylindrical
Invulnerable stages (14)	Absent–present	Absent–present	Present	Absent–present
Invulnerable stages (4)	Absent–present	Absent–present	Present	Absent

* Derived from trait nos 3 and 4.

traits corresponded to the predictions in terms of general trends, but lacked the predicted mixture of trait modalities at low temporal variability (habitat templet area A): 'potential size' (variable 1), 'descendants per reproductive cycle' (variable 2), 'reproductive cycles per year' (variable 3), and 'body flexibility' (variable 12; Table 3). The remaining species traits that were considered did not match predictions (Table 3). Thus, as expected by Townsend & Hildrew (1994), species traits occurred as alternative suites of characteristics in the species of Plecoptera and Ephemeroptera of the Upper Rhône.

Species richness and spatial–temporal habitat variability

The observed distribution of Ephemeroptera and Plecoptera species richness (Fig. 9) does not follow the predictions of the theoretical model. Townsend's (1989) patch dynamics concept, the basis for the hypothesis of Townsend & Hildrew (1994), predicts that species richness peaks at intermediate levels of temporal variation and increases with spatial variability. Highest species richness was observed in the main channel (low spatial and temporal heterogeneity) probably because this is the normal habitat for Plecoptera and most of the Ephemeroptera species.

All other habitats (except for PR–I) show more or less a similar richness (Fig. 9); this implies that each habitat, in spite of the differences in their spatial and temporal variability, offers a similar number of ecological niches available to the Ephemeroptera.

Conclusions

Our analysis of Ephemeroptera and Plecoptera clearly demonstrates that the species traits of the fifty-five species examined by us are related to the habitat types in the Upper Rhône River and its floodplain. The significant relationship between species traits and habitat utilization proves that particular habitat types are used with a particular set of species trait modalities. In addition, the significant trends of species traits along the spatial and temporal axes of the river habitat templet indicate that it is the habitat variability that filters for a particular set of trait modalities. Thus, the general hypothesis of Townsend & Hildrew (1994) that present day habitat conditions in terms of disturbance (= temporal variability) and abundance of refugia (= spatial variability) are matched by present day traits in organisms is clearly supported by our observations. However, as expected by Townsend & Hildrew, trends in only some of the species traits examined

corresponded to those predicted in the river habitat templet.

Predicted trends in species richness in the river habitat templet are not supported by our observations. Two reasons may explain this lack of agreement: perhaps examination of species in only two insect orders is a too narrow 'window' to observe trends in richness; alternatively, biotic interactions may be unimportant for Ephemeroptera and Plecoptera of the Upper Rhône River.

Acknowledgments

References

Berly A. (1988) *Distribution spatio-temporelle des peuplements macrobenthiques prélevés par dragage dans une station du Haut-Rhône.* PhD Thesis, Université Lyon I, 309 pp.

Bohle H.W. (1972) Die Temperaturabhängigkeit der Embryogenese und der embryonalen Diapause von *Ephemerella ignita* (Poda) (Insecta, Ephemeroptera). *Oecologia*, **10**, 253–268.

Bournaud M., Richoux P. & Usseglio-Polatera P. (1992) An approach to the synthesis of qualitative ecological information: the example of aquatic Coleoptera. *Regulated Rivers*, **7**, 165–180.

Bravard J.P., Amoros C. & Pautou G. (1986) Impact of civil engineering works on the successions of communities in a fluvial system. *Oikos*, **47**, 92–111.

Brittain J.E. (1982) Biology of mayflies. *Annual Review of Entomology*, **27**, 119–147.

Brittain J.E. (1990) Life history strategies in Ephemeroptera and Plecoptera. *Mayflies and Stoneflies. Life Histories and Biology* (Ed. I.C. Campbell), pp. 1–12. Kluwer Academic Publishers, Dordrecht.

Brittain J.E. & Lillehammer A. (1987) Variability in the rate of egg development of the stonefly, *Nemoura cinerea* (Plecoptera). *Freshwater Biology*, **17**, 565–568.

Brittain J.E., Lillehammer A. & Saltveit S.J. (1984) The effect of temperature on intraspecific variation in egg biology and nymphal size in the stonefly, *Capnia atra* (Plecoptera). *Journal of Animal Ecology*, **53**, 161–169.

Castella E. (1987) *Apport des macroinvertébrés aquatiques au diagnostic écologique des écosystèmes abandonnés par les fleuves. Recherches méthodologiques sur le Haut-Rhône français.* PhD Thesis, Université Lyon I, 458 pp.

Cellot B., Dole-Olivier M.J., Bornette G. & Pautou G. (1994) Temporal and spatial environmental variability in the Upper Rhône River and its floodplain. *Freshwater Biology*, **31**, 311–325.

Chevenet F., Dolédec S. & Chessel D. (1994) A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology*, **31**, 295–309.

Cogérino L. (1989) *Les rives aquatiques de grands cours d'eau: caractérisation mésologique et faunistique.* PhD Thesis, Université Lyon I, 369 pp.

Degrange C. (1960) Recherches sur la reproduction des Ephéméroptères. *Travaux du Laboratoire Hydrobiologique de l'Université de Grenoble*, **51**, 7–193.

Dolédec S. & Chessel D. (1994) Co-inertia analysis: an alternative method for studying species–environment relationships. *Freshwater Biology*, **31**, 277–294.

Dolédec S. & Statzner B. (1994) Theoretical habitat templets, species traits, and species richness: 548 plant and animal species in the Upper Rhône River and its floodplain. *Freshwater Biology*, **31**, 523–538.

Elliott J.M. (1984) Hatching time and growth of *Nemurella picteti* (Plecoptera: Nemouridae) in the laboratory and a Lake District stream. *Freshwater Biology*, **14**, 491–499.

Elliott J.M. (1987a) Egg hatching and and resource partitioning in stoneflies: the six British *Leuctra* spp. (Plecoptera: Leuctridae). *Journal of Animal Ecology*, **56**, 415–426.

Elliott J.M. (1987b) Temperature-induced changes in the life cycle of *Leuctra nigra* (Plecoptera: Leuctridae) from a Lake District stream. *Freshwater Biology*, **18**, 177–184.

Elliott J.M. (1988) Egg hatching and resource partitioning in stoneflies: ten British species in the family Nemouridae. *Journal of Animal Ecology*, **57**, 201–215.

Elliott J.M. (1991) The effect of temperature on egg hatching for three populations of *Perla bipunctata* (Plecoptera: Perlidae). *Entomologist's Gazette*, **42**, 99–103.

Gaschignard-Fossati O. (1986) *Répartition spatiale des macroinvertébrés benthiques d'un bras vif du Rhône; rôle des crues et dynamique saisonnière.* PhD Thesis, Université Lyon I, 199 pp.

Harper J.L. & Ogden J. (1970) The reproductive strategy of higher plants. I. The concept of strategy with special reference to *Senecio vulgaris* L. *Journal of Ecology*, **58**, 681–689.

Hemphill N. & Cooper S.D. (1983) The effect of physical disturbance on the relative abundances of two filter-feeding insects in a small stream. *Oecologia*, **58**, 378–382.

Hildrew A.G. & Townsend C.R. (1987) Organization in freshwater benthic communities. *Organization of*

of stream community ecology. *Journal of the North American Benthological Society*, **8**, 36–50.

Townsend C.R. & Hildrew A.G. (1994) Species traits in relation to a habitat templet for river systems. *Freshwater Biology*, **31**, 265–275.

Usseglio-Polatera P. (1985) *Evolution des peuplements de Trichoptères et d'Ephéméroptères du Rhône à Lyon (1959–1982). Résultats de piégeage lumineux.* PhD Thesis, Université Lyon I, 451 pp.

Usseglio-Polatera P. (1991) Représentation graphique synthétique de la signification écologique d'un peuplement. Application aux macroinvertébrés du Rhône à Lyon. *Bulletin d'Ecologie*, **22**, 195–202.

Usseglio-Polatera P. (1993) Graphical expression of the ecological significance of faunistical assemblage and its application to the study of the Rhône river Trichoptera at Lyons (France). *Proceedings of the 7th International Symposium on Trichoptera* (Ed. C. Otto), pp. 305–312. University of Umea, Sweden.

Wagner F.H. (1981) Population dynamics. *Arid Land Ecosystems: Structure, Functioning and Management*, Vol. 2 (Eds D.W. Goodall, R.A. Perry & K.M.W. Howes), pp. 125–168. Cambridge University Press, Cambridge.

Webster J.R., Gurtz M.E., Hains J.J., Meyer J.L., Swank W.T., Waide J.B. & Wallace J.B. (1983) Stability of stream ecosystems. *Stream Ecology: Application and Testing of General Ecology Theory* (Eds J.R. Barnes & G.W. Minshall), pp. 355–395. Plenum Press, New York.

Williams D.D. (1984) The hyporheic zone as a habitat for aquatic insects and associated arthropods. *The Ecology of Aquatic Insects* (Eds V.H. Resh & D.M. Rosenberg), pp. 430–455. Praeger Publishers, New York.

Willows R.I. (1987) Population dynamics and life history of two contrasting populations of *Ligia oceanica* (Crustacea: Oniscoidea) in the rocky sublittoral. *Journal of Animal Ecology*, **56**, 315–330.

Wilson D.S. & Keddy P.A. (1986) Species competitive ability and position along a natural stress/disturbance gradient. *Ecology*, **67**, 1236–1242.

Zwick P. (1981) Diapause development of *Protonemura intricata* (Plecoptera: Nemouridae). *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, **21**, 1607–1611.

Appendix 1 Number and name of Plecoptera and Ephemeroptera species collected in the Rhône River and its alluvial floodplain habitats at Brégnier-Cordon and Jons, France, and considered in this analysis

EPHEMEROPTERA
Baetidae
 1 *Baetis atrebatinus* Eaton, 1870
 2 *B. buceratus* Eaton, 1870
 3 *B. fuscatus* (Linnaeus, 1761)
 4 *B. rhodani* (Pictet, 1843)
 5 *B. lutheri* Müller-Liebenau, 1967
 6 *B. muticus* (Linnaeus, 1758)
 7 *B. niger* (Linnaeus, 1761)
 8 *B. pentaphlebodes* Ujhelyi, 1966
 9 *B. pavidus* Grandi, 1949
10 *B. tracheatus* Keffer. & Machel, 1967
11 *B. vernus* Curtis, 1834
12 *Cloeon dipterum* (Linnaeus, 1761)
13 *C. simile* Eaton, 1870
14 *Centroptilum luteolum* (Müller, 1776)
15 *C. pennulatum* (Eaton, 1870)
16 *Raptobaetopus tenellus* (Albarda, 1878)

Caenidae
17 *Caenis macrura* Stephens, 1835
18 *C. luctuosa* (Burmeister, 1839)
19 *C. horaria* (Linnaeus, 1758)
20 *C. robusta* Eaton, 1884

Potamanthidae
21 *Potamanthus luteus* (Linnaeus, 1767)

Heptageniidae
22 *Heptagenia sulphurea* (Müller, 1776)
23 *H. coerulans* Rostock, 1877
24 *Ecdyonurus auranticus* (Burmeister, 1839)
25 *E. dispar* (Curtis, 1834)
26 *E. ruffii* Grandi, 1953
27 *Rhithrogena beskidensis* Alba-Ter. & Sowa, 1987
28 *R. semicolorata* (Curtis, 1834)
29 *Epeorus sylvicola* (Pictet, 1865)

Ephemeridae
30 *Ephemera danica* Müller, 1764

Leptophlebiidae
31 *Habrophlebia fusca* (Curtis, 1834)

32 *H. lauta* Eaton, 1884
33 *Choroterpes picteti* Eaton, 1871
34 *Habroleptoides confusa* Sartori & Jacob, 1986
35 *Paraleptopblebia submarginata* (Stephens, 1835)
36 *Leptophlebia marginata* (Linnaeus, 1767)
37 *L. vespertina* (Linnaeus, 1758)

Ephemerellidae
38 *Ephemerella ignita* (Poda, 1761)

Siphlonuridae
39 *Siphlonurus lacustris* Eaton, 1870
40 *S. aestivalis* (Eaton, 1903)

Oligoneuriidae
41 *Oligoneuriella rhenana* (Imhoff, 1852)

PLECOPTERA
Perlodidae
42 *Perlodes intricata* Pictet, 1841
43 *Isoperla obscura* (Zetterstedt, 1840)
44 *I. grammatica* (Poda, 1761)

Perlidae
45 *Dinocras cephalotes* (Curtis, 1827)
46 *Perla bipunctata* Pictet, 1833
47 *P. burmeisteriana* Claassen, 1936
48 *P. marginata* (Panzer, 1799)

Chloroperlidae
49 *Chloroperla tripunctata* (Scopoli, 1763)
50 *Siphonoperla torrentium* (Pictet, 1841)
51 *Xanthoperla apicalis* Newman, 1836

Leuctridae
52 *Leuctra fusca* (Linnaeus, 1758)
53 *Euleuctra geniculata* Stephens, 1836
54 *Leuctra major* Brinck, 1949

Taeniopterygidae
55 *Brachyptera risi* (Morton, 1896)

Appendix 2 Species traits (nos 1–17 and their modalities (the numbers below the species trait numbers) of Ephemeroptera and Plecoptera used in this analysis (see Table 1 for full labels of traits and modalities and Appendix 1 for species numbers)

```
Species 1    2   3    4    5 6   7          8    9    10 11 12  13  14  15  16          17
(No.)  1234123123412341212312345678910123451234 123 123123 123 123 123 123456789 10 11 123

  1    1300030013030000130300021232100 00130131013131001 3 1030300300003100000 0 1 130
  2    1310030000303000030030332222100 00130122013131001 3 1033000300003100000 0 1 130
  3    1300030003031000300300303323311 0101300132121310013 1031300300003100000 0 1 130
  4    013013301311200030030131223310 0130023102131001 3 103032131310310000 0 1 130
  5    0300030023030000030300122212000 00130013213131001 3 1033000301003000000 0 1 130
  6    0130030003130001300311111222100 0101300231131310013 1033000300003000000 0 1 130
  7    0300310023030001303001221221000 00130013113131001 3 1033000300003000000 0 1 130
  8    0300030003113000303003113320000 0013013102313100 13 1030300301003000000 0 1 130
  9    0300030003013001303003313200000 0130013113131001 3 1030320300003000000 0 1 130
 10    0300030003030000303000111110000 0013001311313100 13 1030300313103000000 0 1 130
 11    1300030003030000303101333333100 1001301320131310013 1030300313102100000 0 1 130
 12    0300230013201300300300123132000 00013131013131001 3 1033100333310310000 0 1 130
 13    1300032003030001303001123123110 0300001320131310013 1033001233203100000 0 1 130
 14    0300130013031001301300111232000 000300032013131001 3 0031110322000000000 0 1 130
 15    0320030013030001303000111211000 0003003311313100 13 0030300311003000000 0 1 130
 16    0300230030003000303000322310000 00030013113130000 3 1033003000000000130 0 1 130
 17    2300300003030001303000131111000 010300122013103003 0013300102300100000 0 1 130
 18    2300230013030001303000131011000 0300101221230030030013300102300100000 0 1 130
 19    3100300003130000303000132210000 0300101210230030030013300103300000000 0 1 130
 20    1300030023030000303000231200000 030000131023003000310032320000000 0 1 130
 21    0030030030031000300001231200000 01031003200330300300013300301121310000 0 1 130
 22    0130030030003001313001133331000 0100200033032130030030310221120310000 0 1 130
 23    0130030030013000303000122310000 0100200033032130030130330022131031 0000 0 1 130
 24    0130030030003001303000132121000 000300023002203003013003022101130200000 0 1 130
 25    0130030030013001303030002311100 0003000220320131003013003011031031 00000 0 1 130
 26    0030030030003000303000123121000 0003002300230300301300302101302000 00 0 1 130
 27    0220030030013000303000132110000 000300012103113003013103003000030000 00 0 1 130
 28    0320032030032000303001231111000 000300012103113003013111000301003200 00 0 1 130
 29    0031003030003001303000003330000 030000220032030030130300030100310000 0 1 130
 30    0003003310003000330000133100000 00300131002300303010313330232000000 0 1 130
 31    0300330030032000303000123110000 03000013101130130013003030130131300000 0 1 130
 32    0300330030023000303000033211000 00031013101301300 13 003030301131300000 0 1 130
 33    0300230032031000303000023220000 00030013101300300130030303033310000000 0 1 130
 34    0030130030003001303003221110000 030010132113003001200331023003103000 00 0 1 130
 35    0030030030013000303011332111000 00030003311310300120033002032101031 00000 0 1 130
 36    0310030030013000303001232100000 03000132113103001200330020321010000 00 0 1 130
 37    0300230030013001303001123210000 03000013211301300120030302032002000 0 1 130
 38    030032003001300130300003110000 0231001210320300300130301311 0330000 0 1 130
 39    0030031030013001303000112110000 0013002320021300030 103030301310300000 0 1 130
 40    0030131030003001303000013110000 0213002320021300030 1030303013103 10000 0 1 130
 41    0130030030013000303000023210000 0100100132132030030 130030213310100000 0 1 130
 42    0023300030003113300003310000 03001003201310301101139300000000132 0 1 103
 43    0130030030031013300011132100 030010023013103003011333030010010230 0 1 103
 44    0030300030031013300113321110 030010023013103003011333030010000230 0 1 103
 45    0013300030003101330001133210000 030010032012003031013003030000000033 0 1 130
 46    0013300300003101330001331000 03001003201200303101200303000000133 0 1 130
 47    0013300030031013300121000 030010032012003031012003030000000133 0 1 130
 48    0013300030003101330011333100 03001003201200303101200303000000000133 0 1 130
 49    030030031000300330000111311 0 03001001302100303101203003002101301000 0 1 103
 50    030030003000030030330133111100 03001001302100300301130303001001001301 1 103
 51    030030003000030033000013100000 030010013021003013010330030021000023 0 0 1 103
 52    030030003000320303000012331 1 10300013121003013010303003001022100010103
 53    033003000003203030000012111 1 1030001312100321301033000300102210001 0 103
 54    033030000032030300000133 0 103000131210032030103300030000221000100 103
 55    032032003000033033001233 10000 01030001301303000310303003020031000010 103
```