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

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SUMMARY

1. For five orders of Insecta (Plecoptera, Ephemeroptera, Odonata, Trichoptera, and Coleoptera) in two sites of the Upper Rhône River (France), the following are examined: (i) relationships among nineteen species traits; (ii) habitat utilization of species; (iii) the relationship between species traits and habitat utilization; and (iv) trends of species traits and species richness in a templet of spatial−temporal habitat variability.
2. The species traits having the highest correlations correspond to reproduction, life cycle, nutritional, and morphological features. Species trait characteristics of Coleoptera are distinctly contrasted with those of Plecoptera and Ephemeroptera; Odonata and Trichoptera are intermediate to these orders.
3. The distribution of species in fourteen habitat types of the Upper Rhône River floodplain demonstrates a transverse gradient from the main channel to the oxbow lakes and the temporary water habitats, and a vertical gradient from interstitial to superficial habitats.
4. Despite a significant relationship between species traits and habitat utilization, superposition between species traits and habitat utilization is limited. At the order level, species form usually one (Ephemeroptera, Trichoptera, Odonata) or several (Coleoptera) groups of relatively homogeneous species traits; however, the species of each of these groups utilize rather different habitat types.
5. Only for some life history traits, e.g. the minimum age of reproduction or the number of reproductive cycles per year, do the trends observed in the framework of spatial−temporal variability of habitat types agree with the predictions from the river habitat templet. This mismatch mainly results from the unique phylogenetic history of the Coleoptera compared with that of the other four orders.
6. Species richness peaks at an intermediate level of temporal variability; however, it does not gradually increase with increasing spatial variability, nor increase from low to intermediate temporal variability.

Introduction

It has long been recognized that rivers and streams are heterogeneous environments (Hynes, 1970) that may be viewed as a mosaic of patches characterized by different environmental conditions (e.g. Pringle et al., 1988; Townsend, 1989; Palmer, O'Keeffe & Palmer, 1991; Townsend & Hildrew, 1994). The dis-tribution of both sedentary and mobile organisms is strongly influenced by the environmental conditions that affect biotic and abiotic processes (see Ward, 1992; Williams & Felmate, 1992, for recent reviews on aquatic insects). Presumably, the faunistic assemblage perceives the spatial and temporal variability of patch mosaics, which is a mechanism that should select for appropriate biological traits and relevant

ecological strategies (e.g. Oswood, 1976; Hildrew & Edington, 1979; Ladle & Ladle, 1992). Therefore, certain combinations of adaptations (especially those for individual survival and reproduction) are assumed to be related to different habitats according to the environmental characteristics of these habitats.

If population dynamics are governed mainly by autecological processes (a basic assumption of Townsend & Hildrew, 1994), a knowledge of species traits of the faunistic assemblage may be used to predict the occurrence of these organisms in a framework of spatial and temporal variability. To examine the potential of this approach, we must identify the link between species traits and the environmental variability.

In this paper, individual species traits of taxa belonging to five insect orders that occur in the aquatic habitats of a large, alluvial floodplain system were determined from autecological information obtained from the literature and unpublished sources (cf. Usseglio-Polatera, 1991, 1993; Bournaud, Richoux & Usseglio-Polatera, 1992). This biological information was then compared with species occurrence (= habitat utilization) in a large range of lotic or lentic habitats at two sites of the Upper Rhône River: Jons and Brégnier-Cordon, France. Thus, the approach of this paper is the same as that taken for individual insect orders in this issue (Richoux, 1994; Tachet, Usseglio-Polatera & Roux, 1994; Usseglio-Polatera & Tachet, 1994). However, the pooling of individual groups of organisms in a common analysis (as done in this paper) has the potential for providing insights that are different from those obtained from analysis of the individual groups. Therefore, the aim of this study was to determine for these five insect orders: (i) relationships among a wide range of species traits; (ii) habitat utilization of species; (iii) relationships between species traits and habitat utilization; (iv) trends of species traits and species richness in a framework of spatial and temporal habitat variability, which are then compared with the predictions of the river habitat templet (Townsend & Hildrew, 1994) and of the patch dynamics concept (Townsend, 1989). To my knowledge, there have been no similar studies that have examined, in this way, relationships between species traits and habitat utilization of Insecta species.

Materials and Methods

Study sites

The sites selected for this study correspond to the most intensively studied sections of the Rhône, namely Jons and Brégnier-Cordon (see Statzner, Resh & Roux, 1994). Jons is a relatively unpolluted site close to Lyon and Brégnier-Cordon is a site that remained almost undisturbed until the river was regulated in 1984 (see Cellot *et al.*, 1994).

Selection of species

The insects sampled in the five orders at the two sites of the Upper Rhône comprise approximately 360 species. Except for Odonata, the species examined for the other four orders of Insecta correspond to those listed in Richoux (1994), Tachet *et al.* (1994), and Usseglio-Polatera & Tachet (1994). Therefore, only the faunal list of the Odonata is presented (Appendix 1). Because the tables of species traits and habitat utilization involve juxtaposition of individual data used for the separate analysis of the Coleoptera, Trichoptera, Ephemeroptera, and Plecoptera, only taxa with reliable information on their species traits were selected: 120 species of Coleoptera, seventy-five species of Trichoptera, forty-one species of Ephemeroptera, fourteen species of Plecoptera, and fourteen species of Odonata (E. Castella, unpublished data). For considerations of species richness, all taxa with reliable determination at the species level were used.

Species traits

Autecological information gathered from a very large and scattered bibliography was reduced to nineteen qualitative or semiquantitative species traits (= variables). For each of these species traits (Table 1), the different modalities (= categories) of 264 species were considered. This information was structured using 'fuzzy coding' (see Usseglio-Polatera, 1991; Bournaud *et al.*, 1992; Chevenet, Dolédec & Chessel, 1994) in the following way: 0, the species had no link with a modality; 1, the species had weak links with the modality; 2, the species was moderately related to the modality; and 3, the species was strongly related to the modality. This technique of fuzzy coding helped to compensate for different types and levels of information available for different species (Chevenet *et al.*, 1994).

When a species trait could be applied to the different stages of the life cycle (egg, larva, pupa, imago), the relative duration of each stage was considered in assigning appropriate scores to the different modalities of a trait (cf. Tachet *et al.*, 1994). Thus, the expression of morphological, physiological, or behavioural traits was standardized for all 264 species. Of the eighteen species traits used in the study of all organisms of the Upper Rhône (Dolédec & Statzner, 1994), only species traits relevant to the Insecta were used in this analysis. In addition, some new species traits that better synthesized nutritional or reproductive strategies were selected: the 'longevity of adults' (variable 5 in Table 1); the 'sex ratio' expressed as the percentage of females (variable 7); the presence of a period of dormancy in the life cycle ('diapause' or quiescence; variable 15); the 'feeding

Table 1 Nineteen species traits (= variables) and modalities (plus their numbers used as labels in the figures) of insects used in this analysis. l, larvae; i, imagines

Variable		Modality		Variable		Modality	
No.	Name	No.	Class	No.	Name	No.	Class
1	Potential size	1	≤5 mm	12	Attachment to	1	Swimmers (l)
		2	>5–10 mm		soil or substrate	2	Crawlers (l)
		3	>10–20 mm		(larvae and	3	Burrowers (l)
		4	>20–40 mm		imagines)	4	Temporary attachment (l)
		5	>40 mm			5	Permanent attachment (l)
2	Potential no.	1	≤100			6	Swimmers (i)
	of descendants per	2	>100–1000			7	Crawlers (i)
	reproductive cycle	3	>1000–3000	13	Body flexibility	1	None (≤10°)
		4	>3000		(larvae)	2	Low (>10–45°)
3	Potential no.	1	<1			3	High (>45°)
	of reproductive	2	1	14	Body form	1	Streamlined (l)
	cycles per year	3	2		(larvae and	2	Flattened (l)
		4	>2		imagines)	3	Cylindrical (l)
4	Potential no.	1	≤1			4	Spherical (l)
	of reproductive	2	2			5	Streamlined (i)
	cycles per individual	3	>2			6	Flattened (i)
						7	Cylindrical (i)
5	Longevity of	1	≤1 day			8	Spherical (i)
	adults	2	>1–10 days	15	Diapause	1	No diapause
		3	>10–30 days			2	Embryonic diapause
		4	>30–90 days			3	Larval diapause
		5	>90–365 days			4	Imaginal diapause
		6	>365 days	16	Feeding habits	1	Shredders (l)*
6	Reproductive	1	Single individual		(larvae and	2	Scrapers (l)
	technique	2	Direct: male and female		imagines)	3	Deposit feeders (l)
7	Sex ratio	1	<50%			4	Filterers (l)
	(% of females)	2	50%			5	Piercers (l)
		3	>50%			6	Shredders (i)
8	Reproductive	1	March			7	Scrapers (i)
	period	2	April	17	Food (larvae)	1	Detritus ≤1 mm
		3	May			2	Detritus >1–10 mm
		4	June			3	Detritus >10 mm
		5	July			4	Living plants ≤1 mm
		6	August			5	Living plants >1–10 mm
		7	September			6	Living plants >10 mm
		8	October			7	Living animals ≤1 mm
		9	November			8	Living animals >1–10 mm
9	Parental care	1	Isolated eggs			9	Living animals >10 mm
		2	Eggs in vegetation	18	Food	1	Detritus ≤1 mm
		3	Cemented aquatic eggs		(imagines)	2	Living plants ≤1 mm
		4	Cemented terrestrial eggs			3	Living plants >1–10 mm
		5	Ovoviviparity			4	Living plants >10 mm
10	Dissemination	1	≤10 m			5	Living animals ≤1 mm
	potential	2	>10–100 m			6	Living animals >1–10 mm
	(larvae)	3	>100–1000 m			7	Living animals >10 mm
		4	>1000–10 000 m			8	Not feeding/assimilating
		5	>10 000 m	19	Respiration	1	Aerial: spiracle, aerial (i)
11	Dissemination	1	≤10 m		(larvae and	2	Aquatic: plastron, aquatic (i)
	potential	2	>10–100 m		imagines)	3	Aquatic: gills, aquatic (l)
	(imagines)	3	>100–1000 m			4	Aquatic: tegument, aquatic (l)
		4	>1000–10 000 m			5	Aerial: spiracle, aquatic (l)
		5	>10 000 m			6	Aerial: spiracle, aerial (l)

* Includes shredding predators.

habits' of larvae and imagines (variable 16), for which the term 'shredders' is used in a different sense than the usual functional feeding group (i.e. 'shredding' predators are included) to avoid a priori correlations with food modalities such as large detritus or living animals.

The species traits 'attachment to soil or substrate' (variable 12) and 'body form' (variable 14) considered both larvae and imagines. However, for the traits 'food' (variables 17 and 18) or 'dissemination potential' (variable 10, which mainly relates to drift, and variable 11), a distinction was made between aquatic and terrestrial stages. The trait 'body flexibility' (variable 13) only refers to larvae. As a result, the species trait matrix consists of 264 species × nineteen species traits, and included 103 relevant modalities. Information on the Odonata is given in Appendix 2.

Habitat utilization

The twenty-two habitat types of the alluvial floodplain of the Upper Rhône River considered in this issue (see Cellot *et al.*, 1994) were defined on geomorphological as well as biological characteristics (Bravard, Amoros & Pautou, 1986). Because not all local imaginal (or subimaginal) dissemination strategies of Insecta species were known, only aquatic stages were coded for the different habitats of Jons and Brégnier-Cordon; this was done based on the information in Castella (1987) for the Odonata and in Richoux (1994), Tachet *et al.* (1994) and Usseglio-Polatera & Tachet (1994) for the other four orders. Existing knowledge on the distribution of Insecta species allowed analysis of only fourteen habitat types (see Fig. 3). This does not correspond to the number of habitat types used in the individual analyses of the different insect orders. For example, Trichoptera occurred in only ten of the fourteen habitat types considered here (cf. Tachet *et al.*, 1994).

For each species, the relative abundance of aquatic larvae and/or adults in the different habitats was considered using the same fuzzy coding technique as used for the species traits (i.e. assigning the affinity of the aquatic stages of a species to the different habitats on a scale from 0 to 3). Therefore, the spatial information consists of a matrix of 264 species × fourteen habitat types.

Data analysis

The two previously introduced matrices (species × traits and species × habitat types) were analysed using methods described by Chevenet *et al.* (1994) and Dolédec & Chessel (1994). First, both matrices were independently processed by correspondence analysis. Then, co-inertia analysis (i.e. the simultaneous ordination of both matrices) was used to check for a relationship between species traits and habitat utilization. Following the above analysis, trends in species traits and species richness were examined in the framework of spatial and temporal variability that was based on physical and chemical criteria (see Cellot *et al.*, 1994).

Results

Relationships among species traits

The diagram of eigenvalues indicates the importance of the first axis in explaining the variability of total inertia (16.7%) in the correspondence analysis of the fuzzy coded species traits (Fig. 1a). The axis F2 explained one-half (8.3%) of the variability of the first axis. The distribution of families at the mean of their species locations in the factorial plane F1 × F2 supports the systematic adherence of each family to the different orders (Fig. 1b). This indicates the relative homogeneity in the species traits in a given order, and that these traits are clearly separated from those displayed by species of other orders. A major structure is emphasized by the first axis, which distinctly opposes Coleoptera species (F1 > 0) and Plecoptera or Ephemeroptera species (F1 < 0). Odonata and Trichoptera species exhibit an intermediate location.

Correlation ratios permit the species traits that are best explained by successive factorial axes to be identified (Fig. 2). The species traits having the highest correlation ratios on axis F1 correspond to reproduction or life cycle (variable 2: 'potential number of descendants per cycle'; variable 4: 'potential number of cycles per individual'; variable 5: 'longevity of adults'), or nutritional (variable 16: 'feeding habits'; variable 18: 'food' of imagines) characteristics (correlation ratios between 0.55 and 0.82). Modalities of the species traits 'size' (variable 1), 'body flexibility' (variable 13), 'body form' (variable 14) and 'respiration' (variable 19) are relatively well separated by the first axis (ratios 0.39−0.45). The species traits 'size', 'potential number of descendants per cycle', 'feeding habits', 'food' of larvae (variable 17), and 'food' of imagines are relatively widely spread along the second axis (ratios 0.34−0.56).

Trait modalities of two faunal groups are opposed on axis F1 (cf. the position of trait modalities in Fig. 2 with that of families in Fig. 1b). At the positive side (group I), very small to medium-sized species (variable 1), with low fecundity (variable 2) but a long-lived imaginal stage (variable 5) that enables several reproductive cycles per individual (variable 4) occur. These species, which can reproduce early in the year (variable 8), have low dispersal abilities (variables 10 and 11). The adult stages, which have a functional digestive system, feed on particulate detritus, plants,
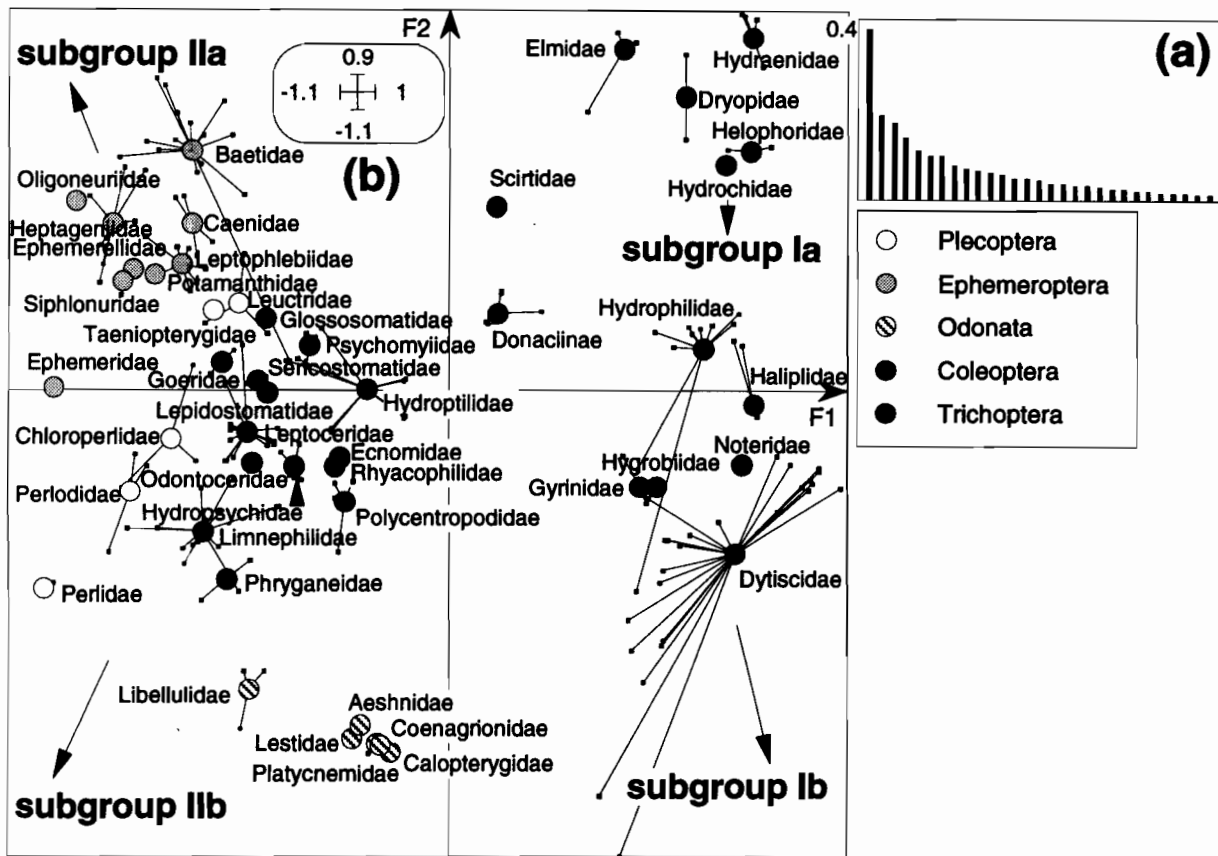
Fig. 1 Ordination of species traits by correspondence analysis. (a) Histogram of eigenvalues. (b) Distribution of families (circles) of the five Insecta orders on the F1 × F2 plane that are positioned at the weighted average of their species (small squares). Lines link species to their families (see text for discussion of subgroups).

or animals (variable 18). Most larvae are carnivorous (variable 17). Group I corresponds to Coleoptera (Fig. 1b). At the negative side (group II), species with short-lived imagines (with only one reproductive cycle per individual) having a small to large potential size and a high fecundity occur. For larvae and adults, the potential of dissemination is higher than that found in group I. The adult stage is not feeding, and larvae can use different sources of food, The hemimetabolous Plecoptera, Ephemeroptera, and Odonata, and the holometabolous Trichoptera species belong to group II (Fig. 1b).

The second axis (F2) adds structure to that highlighted by the first axis (Fig. 2). In group II, the species located at the positive side of the F2 axis (subgroup IIa; Fig. 1b) exhibit a small size and the shortest adult longevity but have the highest fecundity and several reproductive cycles per year. Parthenogenesis is frequent (variable 6), and females often predominate

in the sex ratio (variable 7). Scrapers or deposit feeders are dominant in the larvae (variable 16), and their food is represented by fine living plants and/or detritus particles (variable 17). The adults do not feed (variable 18). The subgroup IIa mainly consists of Ephemeroptera species, with Baetidae, Caenidae, and Heptageniidae being the main components of this subgroup (Fig. 1b). At the negative side of the F2 axis, the subgroup IIb corresponds to organisms having a larger size but a lower fecundity, and a longer generation time (semi- or univoltinism) with a longer adult life duration (from 10 to 90 days). If the sex ratio departs from the 50:50 ratio, males are often dominant. Imagines may feed on living animals, and shredders or filterers and dominant among the larval stages using coarse particulate organic matter (detritus, living plants, and animals). Species of Odonata, the Plecoptera suborder Setipalpia (Perlidae, Perlodidae, and Chloroperlidae) and
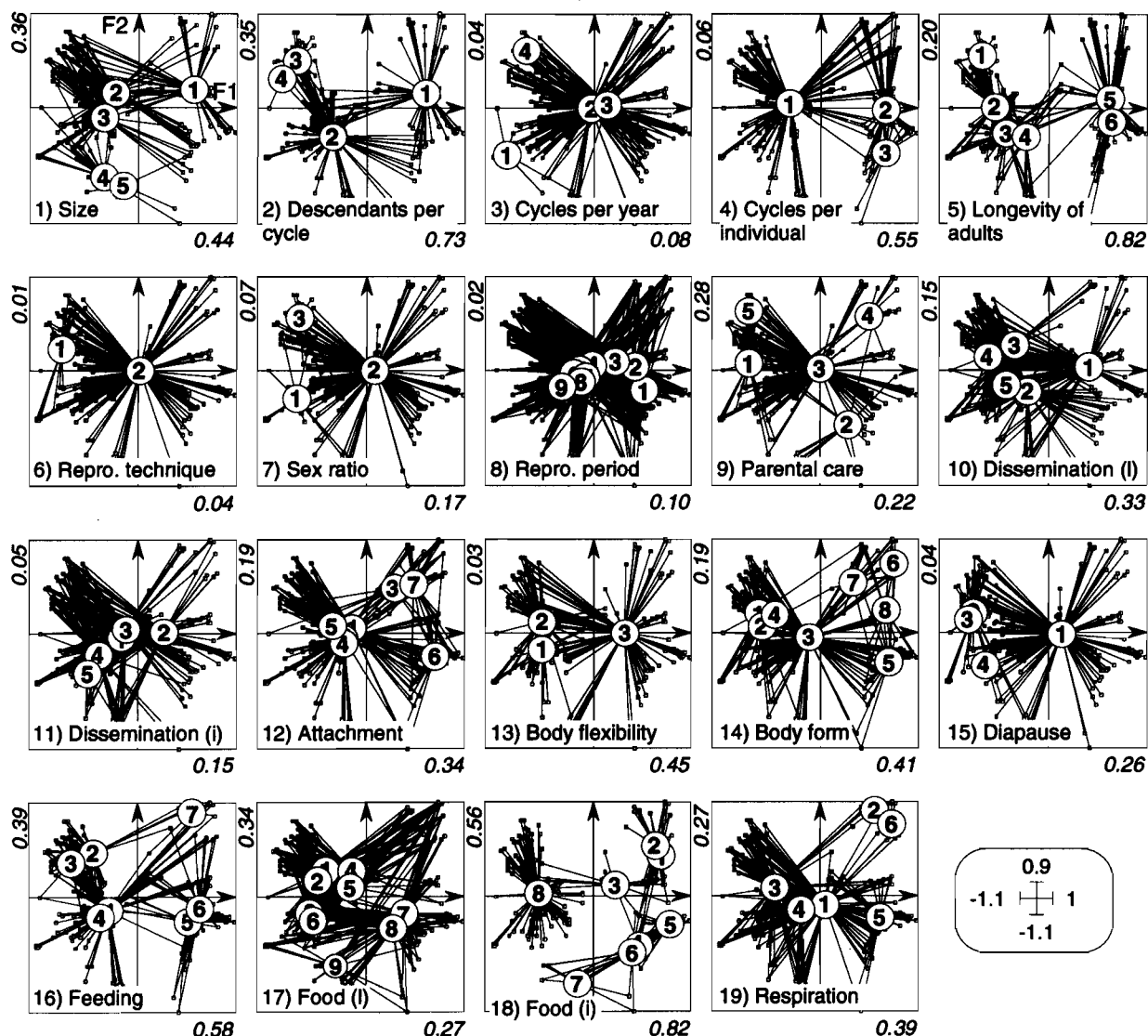
Fig. 2 Ordination of species traits by correspondence analysis. Distribution of modalities (the numbers in circles) of nineteen species traits on the F1 × F2 plane, with correlation ratios for each species trait indicated on the axes (see Table 1 for full labels of species traits and trait modalities; 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.

Trichoptera (Limnephilidae, Phryganeidae, and Hydropsychidae) belong to this subgroup (Fig. 1b).

The species of the group I are mainly arranged along a gradient of size, from the small Elmidae and the Hydraenidae (positive side of the F2 axis, subgroup Ia) to the Dytiscidae (negative side of the F2 axis, subgroup Ib; Fig. 1b and 2). These mainly differ in the species traits of their imaginal stages. The extremes of group I range in the adults from the crawlers (variable 12), scrapers (variable 16), and

users of fine living plants or detritus (variable 18; subgroup Ia), to swimmers, shredders, and those that feed on living animals (subgroup Ib).

Habitat utilization

The eigenvalue diagram from the correspondence analysis of the habitat utilization matrix emphasizes the importance of the two first axes (Fig. 3a), which explain 22.7% (F1) and 18.0% (F2) of the total inertia.
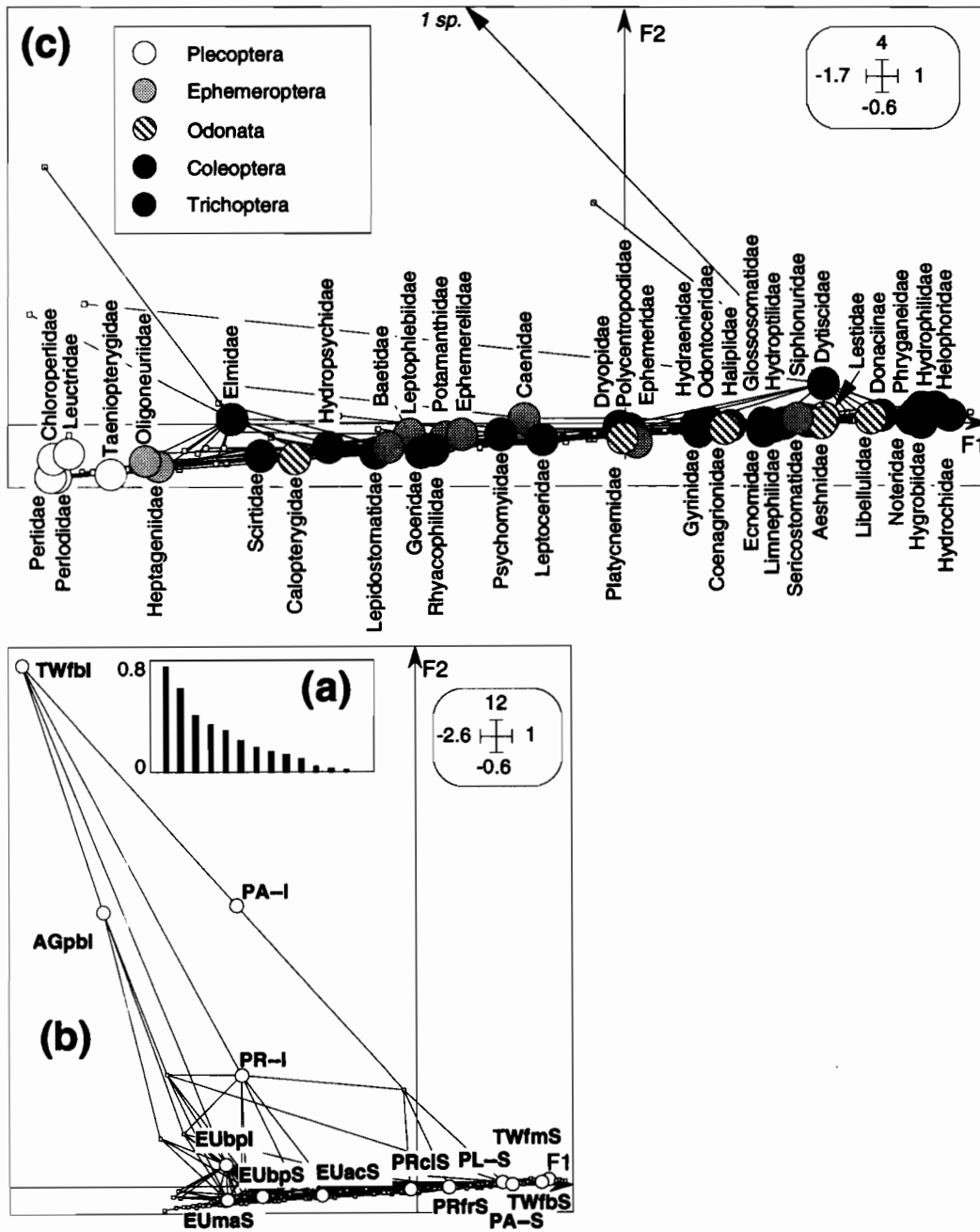
Fig. 3 Ordination of habitat utilization by correspondence analysis. (a) Histogram of eigenvalues. (b) Distribution of fourteen habitat types (circles) on the F1 × F2 plane. Small squares represent the species. Each circle is positioned at the weighted average of species found in that habitat type. Lines link species to habitat types. Habitat type identifiers (five characters; 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); TW, temporary water; —xx–: –, no specification; ac, artificial channel; bp, bypassed section; cl, close to the main channel; fb, former braided channel; fm, former meander or anastomosed channel; fr, far from the main channel; ma, meander or anastomosed or main channel; pb, pebble; ——X: I, interstitial; S, superficial. (c) Distribution of families (circles) of the five Insecta orders on the F1 × F2 plane that are positioned at the weighted average of their species (small squares). Lines link species to their families.

The F1 scores for the different habitat types of the two Upper Rhône sites clearly demonstrate a transverse gradient (Fig. 3b), with the superficial habitats organized along the F1 axis in terms of their relation with the main channel, i.e. from the active main channel (EUmaS) to the paleopotamon (PA−S) and the temporary waters (TWfmS, TWfbS). All of the families in the five orders examined, which are located at the mean of their species distributions, are arranged along this transverse gradient in Fig. 3c. The five rheophilous families of Plecoptera, the Heptageniidae and Oligoneuriidae of the Ephemeroptera, and the Elmidae and Scirtidae of the Coleoptera are the most typical forms of eupotamic habitats. Other taxa are more representative of lentic or stagnant environments, such as certain Coleoptera (Hydrochidae, Helophoridae, Hygrobiidae, Hydrophilidae or Noteridae), Trichoptera (Phryganeidae), or Odonata (Libellulidae, Aeschnidae, Lestidae) families. The second factorial axis separates the superficial from the interstitial habitats (Fig. 3b). The ordination of interstitial habitats corresponds to their relation to the main channel, from the eupotamon (low F2 scores) to the temporary waters (elevated F2 scores).

Relationship between species traits and habitat utilization

A co-inertia analysis was used to investigate the relationship (= co-structure) between species traits and the habitat utilization of the species. A permutation test (Dolédec & Chessel, 1994) indicated that the co-structure between species traits and habitat utilization was significant ($P < 0.005$) for the first and second axis of the co-inertia analysis.

The projection of axes of inertia of the separate analyses (species traits and habitat utilization) on the co-inertia axes indicates that the axes of co-inertia (plane F1 × F2) mainly express the structure of plane F1 × F2 for the species traits (Fig. 4a) and of the planes F1 × F4 and F1 × F5 for the habitat utilization (Fig. 4b). As in Fig. 3b, a habitat ordination according to their relation to the active channel is found along the F1 axis (Fig. 4c), from the main channel (EUmaS) and its more or less artificial variants (EUbpS, EUbpI, EUacS) to the plesiopotamic (PL−S) or paleopotamic (PA−S, PA−I) habitats and the temporary waters (TWfmS, TWfbS, TWfbI).

As in the separate analysis of species traits, the
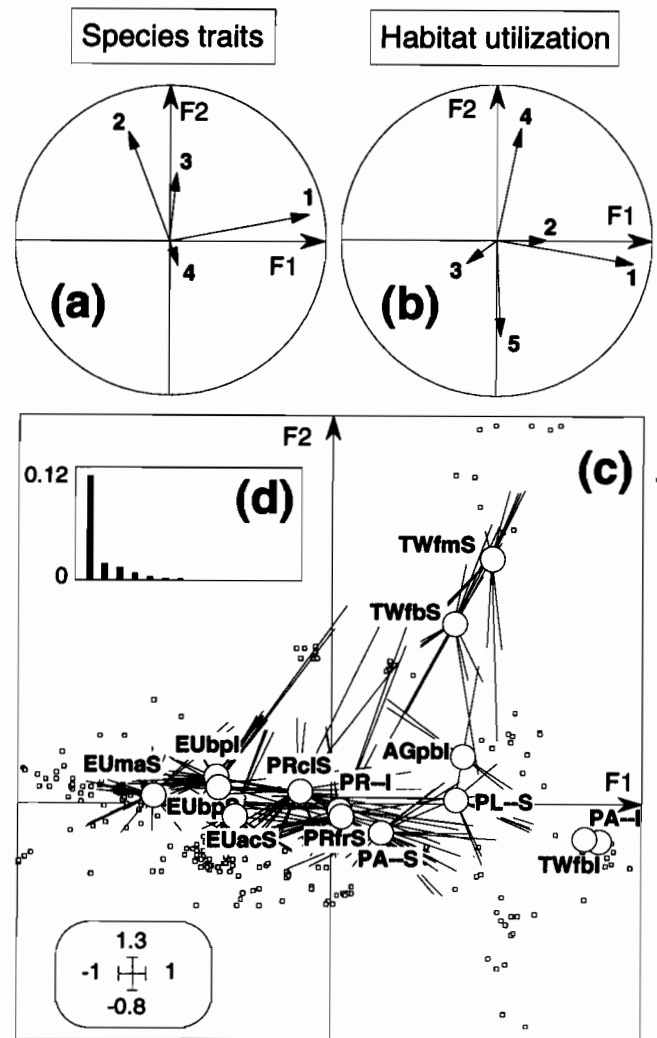
Fig. 4 Co-structure between species traits and habitat utilization by co-inertia analysis. (a & b) Relationships between separate analyses and co-inertia analysis. Each arrow represents an axis number of the standard analysis (species traits or habitat utilization) that are projected on to the co-inertia axes (F1 and F2). (c) Ordination of habitat types (circles) on the F1 × F2 plane with species (small squares) positioned according to their species traits (see Fig. 3 for further details). Lines link species to their habitat types but are only 50% of their total length for readability; lines are omitted if a species contributed less than 1% to the habitat type distribution. (d) Histogram of eigenvalues.

most relevant (cf. high correlation ratios in Fig. 5) traits for the co-structure correspond to reproduction (variable 2: 'potential number of descendants per cycle'; variable 3: 'potential number of cycles per year'; variable 4: 'potential number of cycles per individual'; variable 5: 'longevity of adults'), morphological (variable 14: 'body form') or behavioural

(variable 16: 'feeding habits'; variable 10: 'dissemination potential' of larvae) aspects. The co-inertia analysis separates semivoltine but highly fecund species with strong larval dissemination potential from uni- or polyvoltine species with reduced fecundity and reduced mobility capacities. The former, which are more typically for eupotamic environments (cf. Fig. 4c), have larval body forms adapted to the current (variable 14), larvae that are specialized in their 'feeding habits' (scrapers, filterers; variable 16) and can possibly avoid adverse abiotic conditions

(especially high temperatures or droughts in the summer, or spates in the autumn) by having a phase of embryonic or larval dormancy (variable 15). The latter, which are less adapted to flow as larvae, are shredders (adults and larvae) or piercers (larvae), and possibly avoid harsh aestival periods by having an imaginal diapause (Fig. 5). These species more typically occur in habitats that are rarely connected with the main channel (plesiopotamon, paleopotamon, and temporary waters; Fig. 4c).

These characteristics in species traits along the

Fig. 5 Co-structure between species traits and habitat utilization by co-inertia analysis. Ordination of species traits on the F1 × F2 plane with species (small squares) positioned according to their habitat utilization (see Fig. 2 for further details). Lines link species to their modalities but are only 50% of their total length for readability; lines are omitted if a species contributed less than 1% to the modality distribution.

transversal habitat gradient can be related to the various families through Fig. 6 (cf. the position of families in Fig. 6 with that of trait modalities in Fig. 5 and that of habitat types in Fig. 4c). However, it should be noted that the families are often more uniform (i.e. the species are closer to their family circle) when positioned by species traits (as in Fig. 6) than when positioned by habitat utilization (not shown). Fig. 7 focuses on this topic at the species level for the five insect orders. On the factorial map of the co-inertia analysis, each species is defined as a vector plotted between its habitat utilization score (the beginning of the arrow) and its trait score (the end of the arrow). Although significant globally (see above), the various insect groups have only a limited co-structure between species traits and habitat utilization because there is a limited superposition of the species when positioned by species traits and by habitat utilization (most of the arrows

are relatively long, Fig. 7). The Trichoptera, Ephemeroptera, and Odonata exhibit a wide spatial distribution even though their species traits are quite homogeneous (demonstrated by the convergence of the ends of the arrows). The Plecoptera, which have slightly less homogeneous species traits, have a restricted habitat utilization (mainly the main channel). The Coleoptera, when taken as a whole, have both a wide spatial distribution and a variety of species traits. However, if divided into two groups of families with about the same number of species (for better readability of the information) several zones of convergence of species traits appear to exist in the Coleoptera (Fig. 7).

Species traits, species richness, and spatial–temporal habitat variability
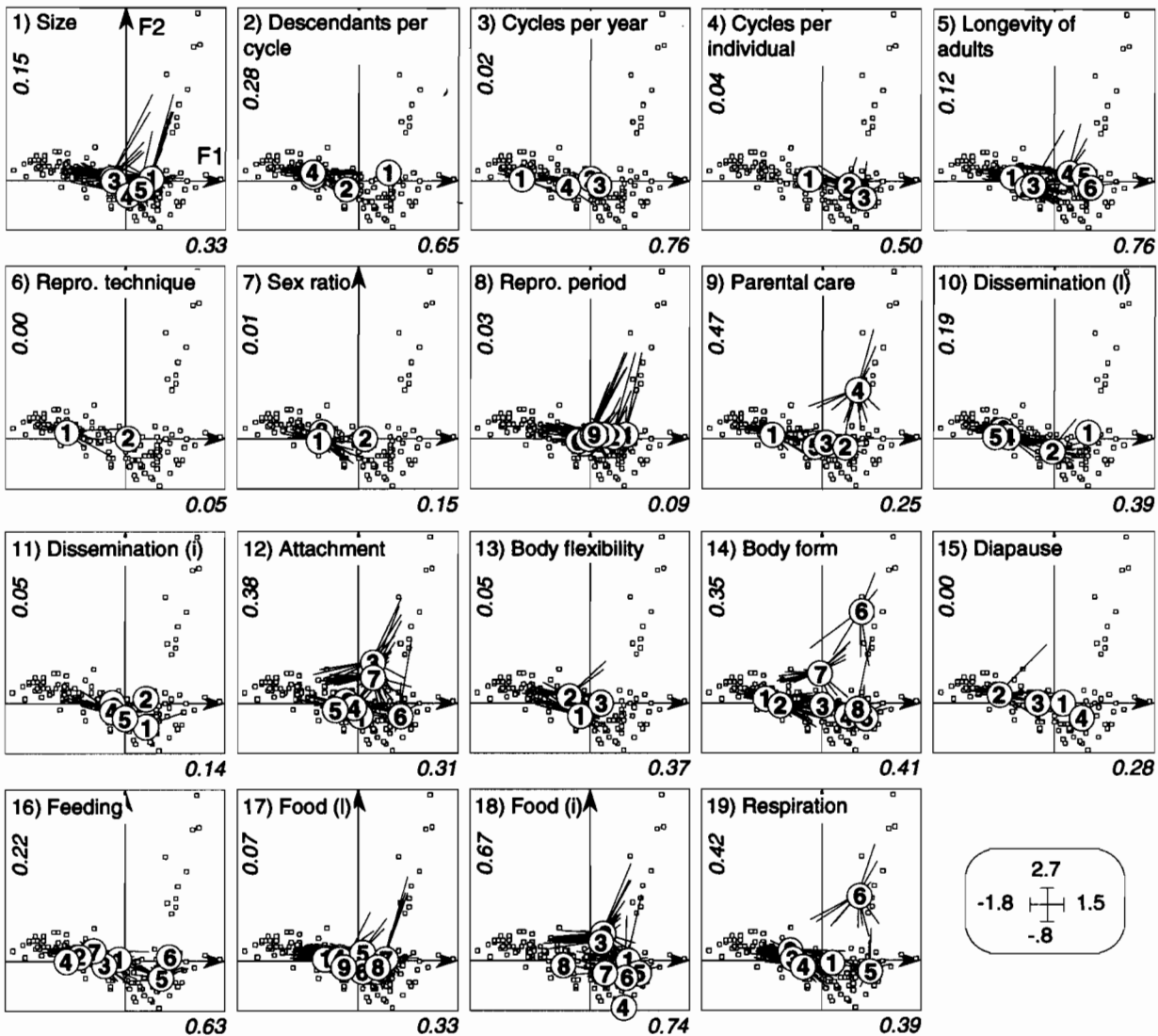
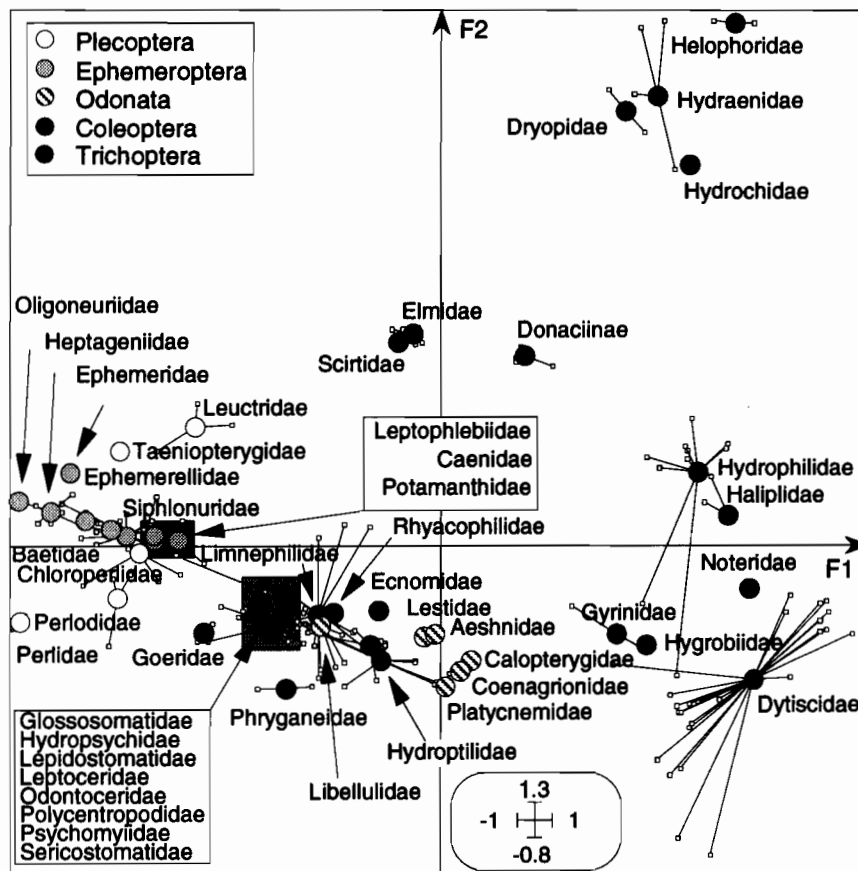If the fourteen different habitat types are positioned

Fig. 6 Co-structure between species traits and habitat utilization by co-inertia analysis. Ordination of families of the five Insecta orders on the F1 × F2 plane according to their species traits (see Fig. 1 for further details).
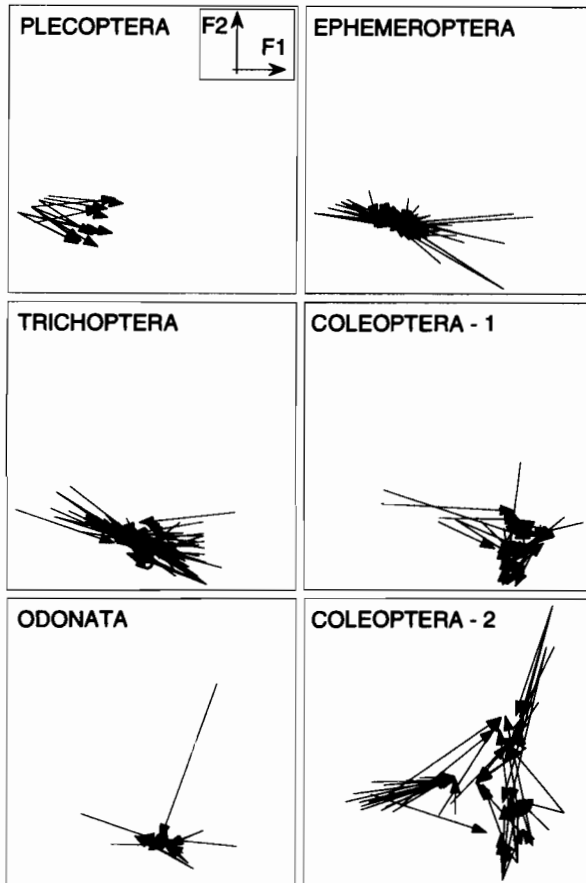
Fig. 7 Comparison of species positions on the two F1 × F2 planes by co-inertia analysis (see Fig. 4d for eigenvalues). Each species is defined by an arrow. The beginning of the arrow marks the position according to the habitat utilization of a species and the end of the arrow marks its position according to the species traits. Haliplidae, Hygrobiidae and Dytiscidae species are gathered into Coleoptera—1; species of other families into Coleoptera—2.

in the framework of spatial and temporal variability (Fig. 8a), the eupotamic and interstitial environments (apart from the bypassed sections: EUbpS) have the lowest spatial and temporal variability. Two other habitats (PA—S, TWfmS) exhibit low to intermediate spatial variability and intermediate (if compared with all twenty-two habitat types in Cellot *et al.*, 1994) temporal variability. The spatial variability is high in four habitat types (PRfrS, PRclS, PL—S, TWfbS), which correspond to the intermediate area of the transverse floodplain gradient. The temporal variability of those habitats is also intermediate. Except for the bypassed sections, the temporal varia-

bility increases from the main channel to temporary waters along the transversal gradient (Fig. 8a).

The distribution of species and families in the framework of spatial—temporal variability is illustrated in Fig. 8b. The five families of Plecoptera occupy the habitats with the lowest spatial—temporal variability; their species are opposite several mayfly, beetle, and caddisfly families (the Siphlonuriidae, Hydraenidae, Haliplidae, Donaciinae, Noteridae, Hydrophylidae, Dytiscidae, and Limnephilidae), which mainly occur in environments with a high spatial and intermediate temporal variability. Other Insecta families use either a relatively restricted part of this templet (e.g. Heptageniidae or Hydropsychidae) or are scattered throughout the templet (e.g. Baetidae or Leptoceridae).

A permutation test (Chevenet *et al.*, 1994) indicated that trends in species traits are significant ($P < 0.005$) along the axis of spatial and temporal variability of the river habitat templet.

Most of the different modalities of the species traits are ordinated parallel to a gradient of increasing spatial and temporal variability (Fig. 9). There is a trend of decreasing fecundity (variable 2) and larval dissemination abilities (variable 10) but an increase in the annual number of generations (variable 3) and adult life duration (variable 5) as spatial and temporal variability increase (Fig. 9). A shift from reproduction by a single individual (parthenogenesis) to that by mating males and females (variable 6), a decrease in the attachment to the substrate (variable 12), a widening of possible sources of food (e.g. the opposition between specialists as filterers or scrapers and generalists as shredders, variable 16) and a modification in body form (variable 14) are also observed along this gradient.

Finally, species richness, defined as the total number of Insecta (larvae and/or imagines) species collected in the two sites, was projected on each habitat type using the same bidimensional framework of spatial and temporal variability (Fig. 10). Species richness tends to increase with increasing temporal and spatial variability; however, exceptions occur (e.g. TWfbS habitats), and highest species richness is found in the superficial paleopotamon (PA—S), which is at a relatively high temporal variability but relatively low spatial variability.

Baetidae

Siphlonuridae
Ephemeridae
Caenidae
Potamanthidae
Heptageniidae

Ephemerellidae
Leptophlebiidae
Oligoneuriidae

Perlidae
Perlodidae
Chloroperlidae
Leuctridae
Taeniopterygidae

Polycentropodidae

Hydroptilidae

Limnephilidae
Phryganeidae
Hydropsychidae

Leptoceridae

Dytiscidae

Haliplidae
Helophoridae

Sericostomatidae
Odontoceridae
Glossosomatidae
Psychomyiidae
Goeridae Ecnomidae
Rhyacophilidae
Lepidostomatidae

Noteridae
Dryopidae
Gyrinidae
Hygrobiidae

Hydraenidae
Hydrochidae

Hydrophilidae

Donaciinae
Elmidae
Scirtidae

Libellulidae
Lestidae
Coenagrionidae
Platycnemididae
Aeshnidae
Calopterygidae

(b)

Spatial variability
0.30
0.20
0.10
0
Temporal variability
0   0.05 0.10 0.15

○ Plecoptera
◎ Ephemeroptera
◉ Odonata
● Coleoptera
● Trichoptera

(a)

Spatial variability
0.30
0.20
0.10
0

PRcIS
PL–S
TWfbS
PRfrS
PA–S
EUmaS PR–I TWfmS EUbpS
EUacS AGpbI EUbpI
PA–I TWfbI

0   0.05   0.10   0.15
Temporal variability

Fig. 8 Habitats and families of five insect orders in the templet of spatial–temporal habitat variability. (a) Ordination of habitats in the templet of spatial–temporal habitat variability (see Fig. 3 for habitat identifiers). The templet axes indicate cumulated variability of factorial scores for eight environmental variables. (b) Distribution of species and families in the same templet (see Fig. 1 for further details).

Discussion

Relationships among species traits

The higher systematic unit of the species is a major feature for the ordination of species traits found in this analysis (Fig. 1b). For each systematic group, there is a strong linkage among species belonging to that group relative to the location of species belonging to other groups. For example, Coleoptera species are totally separated from species of the other four orders. Odonata incorporate relatively specific features. And the Ephemeroptera, Plecoptera, and Trichoptera have more similar species traits, although they are somewhat distinct (along the axis F2, Fig. 1b).

Some of the general reasoning in the predictions of Townsend & Hildrew (1994) is derived from the $r-K$
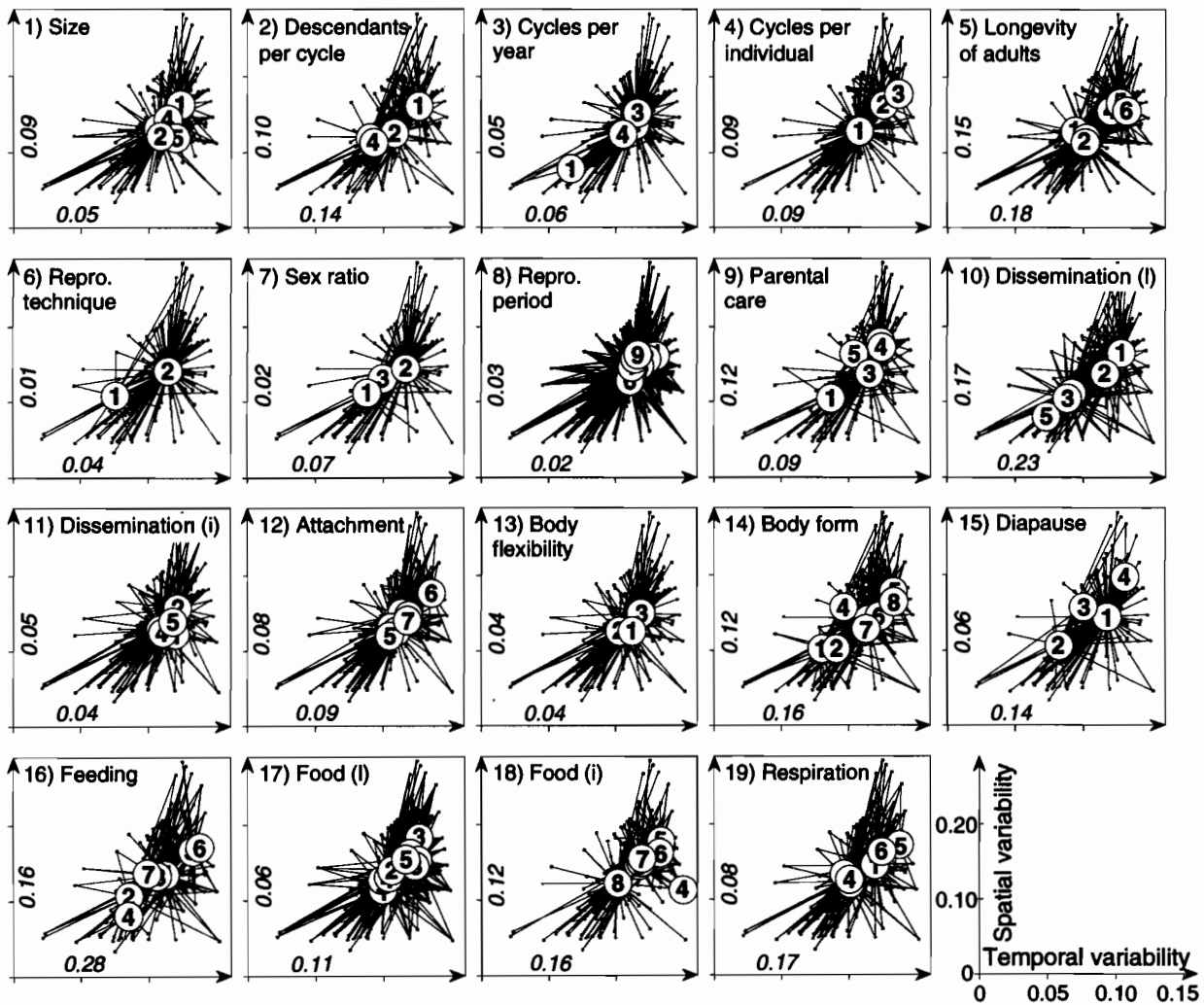
Fig. 9 Species traits in the templet of spatial–temporal habitat variability. Species (small squares) are positioned at the weighted average of their habitat utilization and each modality (the number in a circle) is positioned at the weighted average of species representing that modality (see Fig. 2 for further details).

concept. However, consideration of all 264 Insecta species demonstrates no simple $r-K$ gradient in the species traits (Figs 1 and 2). The major structure emphasized by the first axis partly corresponds to a relative $r-K$ gradient from the Ephemeroptera towards the Coleoptera because the separation among species is partly based on reproductive traits (variables 2, 3 or 4). The 'number of descendants per reproductive cycle' decreases and the 'number of reproductive cycles per individual' increases along this gradient, corresponding to patterns predicted by the $r-K$ concept. In contrast to these predictions, the 'number of reproductive cycles per year' can be low or very high on the r side, and relatively high on the

K side of the gradient of the previous two species traits. If one considers 'size' (variable 1) and 'longevity of adults' (variable 5), two traits that also can be used for the characterization of relative $r-K$ gradients, the picture becomes more complicated because the long-living Coleoptera are relatively small. Focusing on the 'number of descendants per reproductive cycle', which is the most important trait with respect to the reproduction potential (cf. the modality limits in Table 1), the aquatic Coleoptera, as has been emphasized by Richoux (1994), may be considered as K strategists and both the hemimetabolous orders (Plecoptera, Ephemeroptera, and Odonata) and the holometabolous Trichoptera may be considered as

Fig. 10 Species richness of the five Insecta orders 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).

preserved at the class level if the species trait heterogeneity in the order is high. If treated at the class level, the positions of Ephemeroptera, Plecoptera, Odonata, and Trichoptera became quite homogeneous (on the F1 × F2 plane of the analysis), and only Coleoptera exhibit the same species' trends already displayed at the order level (cf. Richoux, 1994). The pattern is the same because an opposition between the most important part of the Hydradephaga and the Hydrophilidae (group II of Richoux, 1994) and the other groups (groups I and III of Richoux, 1994) is found. This relates to the greater heterogeneity of the Coleoptera compared with the other insect orders in their modality characteristics; consequently, the Coleoptera define the major part of the variability of the species trait framework. Finally, in the overall analysis that considers 548 plant and animal species of the Upper Rhône (Dolédec & Statzner, 1994), Insecta display a quite homogeneous position because the range of species trait variability is again increased. Consequently, a study at a lower systematic level (e.g. order) should be viewed (and used) as a magnifier of apparently homogeneous patterns found at a higher systematic level (e.g. class).
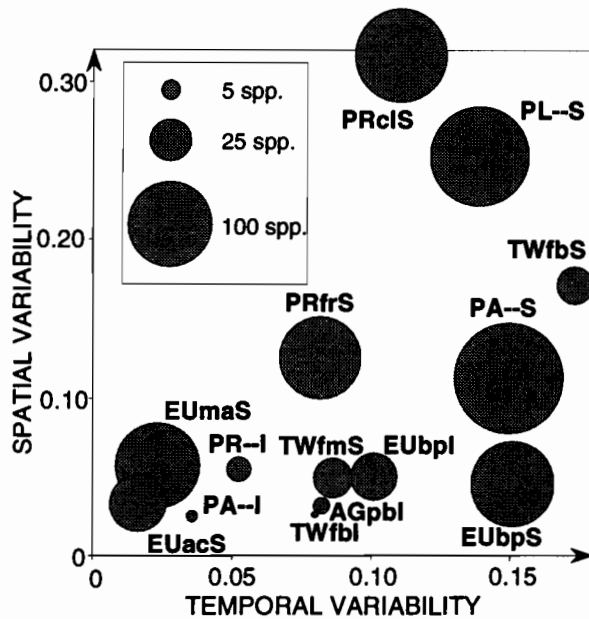
Habitat utilization

As underscored by the individual order-level analyses (Richoux, 1994; Tachet *et al.*, 1994; Usseglio-Polatera & Tachet, 1994), both a vertical (from interstitial to superficial habitats) and especially a transverse gradient are discriminated by the ordination of habitats (Fig. 3). The applicability of the river typology initially developed on geomorphological and biological considerations by Bravard *et al.* (1986) is thus confirmed. Plecoptera are dominant in the superficial habitats of the main channel. Trichoptera, Ephemeroptera, and Elmidae (Coleoptera) are dominant in most lotic habitats of the eupotamon; Odonata occur mainly in para- and paleopotamic environments; and Coleoptera, which are present in all types of freshwater habitats, also occupy temporary waters.

Relationship between species traits and habitat utilization

There is a general gradient in species traits and the habitats in which these traits occur, from lotic to lentic environments, for both interstitial and super-

r strategists. Furthermore, the observed gradient (along the second axis) also corresponds to a contrast between: (i) species that in general have a clear *r* reproductive strategy (positive F2 scores) and should be more effective in new or disturbed habitats; and (ii) species that in general have a less pronounced *r* reproductive strategy (negative F2 scores).

Because the *r*–*K* concept is related to relative gradients, an expected observation is that the *r*–*K* assignment of a given group depends on the systematic units considered. For example, in the study of Plecoptera and Ephemeroptera species (Usseglio-Polatera & Tachet, 1994), the distribution of modalities in species traits on reproductive/colonization characteristics demonstrates that the Plecoptera tended to the *K* side when compared with the Ephemeroptera (Plecoptera are less fecund, have a slower larval development, and a lower investment in colonization abilities than Ephemeroptera). If one examines the distribution of modalities in species traits at the class level (Insecta), Plecoptera belong to the group II that tends towards *r* strategy. In addition, it is clear that the organization of the different species' locations on the F1 × F2 plane of the analysis within a systematic unit such as an order has a higher chance of being

ficial habitats (Figs 4 and 5). For Ephemeroptera, Trichoptera, and Odonata, the ordination of species indicates a higher variability in the position of species according to habitat utilization than in the position of species according to species traits (Fig. 7); this indicates that species of these three orders use a variety of habitat types despite having very similar species traits. In contrast, Plecoptera, which use a reduced number of lotic habitat types, have rather heterogeneous species traits. Finally, Coleoptera occur in different habitat types with very different species traits.

However, the strong organization of species trait modalities and their gradual shift from the main channel towards the temporary waters demonstrates: (i) the relevance of traits such as 'number of descendants per reproductive cycle' (variable 2), 'number of cycles per individual' (variable 4), 'longevity of adults' (variable 5), larval or imaginal 'dissemination potential' (variables 10 and 11), 'attachment to soil or substrate' (variable 12), 'body flexibility' (variable 13), 'body form' (variable 14), 'diapause' (variable 15) or 'feeding habits' (variable 16) for the habitat utilization; and (ii) clear limitations in the habitat utilization for most of the species.

Species traits and spatial—temporal variability

As presented in the Introduction, the species assemblage in a particular environment is assumed to perceive spatial and temporal heterogeneity. Species react to this fluctuating environment by appropriate biological and/or ecological characteristics, which will depend on a species' ability to modify a combination of their species traits. How a given organism reacts will depend on the constraints on its morphology, physiology, and behaviour; all of these constraints result from its phylogenetic history (e.g. Southwood, 1988; Townsend & Hildrew, 1994). As a result, environmental patchiness may have major consequences on the outcome of autecological processes (species/environment) or competitive interactions among species. In this context, temporal variability is considered as an indicator of the frequency of disturbance and spatial variability as an indicator of abundance of refugia, with the latter being a buffer against the former (Townsend & Hildrew, 1994).

The species trait predictions made by Townsend &

Hildrew (1994, Fig. 4) are based on a partition of the habitat templet into two areas labelled A and B. Area A corresponds to low temporal variability and area B refers to high temporal variability; the spatial variability modifies the transition between these two areas. According to the predictions of the theoretical construct (see Table 2, or Table 1 in Townsend & Hildrew, 1994), species traits in area A are more often a mixture of different features than in area B, where traits are generally represented by only a single feature. This is based on the assumption that species trait modalities enabling successful exploitation of temporally variable habitats are also present in more stable habitats along with a wide variety of other modalities. In fact, because of the high number (264) and variety of insect species, the analysis showed that most of the modalities of the species traits occur in all the habitats studied regardless of their temporal or spatial variability (Fig. 9). However, it is possible to check for the trends in observed modality positions against the trends predicted from the theoretical construct (Table 2).

Only the life history traits 'minimum age at reproduction' [derived from the 'number of reproductive cycles per year' (variable 3), the 'number of reproductive cycles per individual' (variable 4), the 'longevity of adults' (variable 5) and 'diapause' (variable 15)] and the 'number of reproductive cycles per year' (variable 3) are in agreement with the predictions from the river habitat templet (Table 2). In the same way, a stressed specialization in 'feeding habits' (variable 16) is observed in more stable environments (Fig. 9). This specialization is an expected outcome of a stronger competition for the available food resources (Southwood, 1988; Townsend & Hildrew, 1994).

In contrast, fecundity (variable 2) and the total 'number of cycles per individual' (variable 4) do not match the predictions from the river habitat templet (Table 2, Fig. 9). This mainly results from the position of many Coleoptera species in the framework of spatial and temporal variability (Fig. 8b). These beetles have both homogeneity in their reproductive traits (long life duration, low fecundity, several reproductive cycles per individual) and high imaginal colonization abilities, which enable them to use temporally unstable habitats in both larval and adult phases; they occur together in these habitats with typical *r* strategists (Hydroptilidae, some species of

Table 2 Trends in species traits predicted in areas A and B of the river habitat templet (Townsend & Hildrew, 1994) and observations for the five Insecta orders in the Upper Rhône on traits for which predictions were available. If several modalities are observed in an area for a species trait, the dominant modality is in italics. l, larvae; i, imagines

Species trait	Habitat templet area A		Habitat templet area B	
	Predictions	Observations	Predictions	Observations
Minimum age at reprod.*	Old–young	Old–young	Young	Young
Descendants per cycle (variable 2)	Few–many	Many	Many	Many–*few*
Cycles per year (variable 3)	<1–several	<1–several	Several	Several
Longevity† (l + i)	Long–short	*Long*–short	Short	Long–short
Size (variable 1)	Large–small	Large–small	Small	Large–*small*
Cycles per individual (variable 4)	Many–one	One	Few–one	*Few*–one
Parental care (variable 9)	Present–absent	Present–absent	Absent	Present–absent
Reprod. technique (variable 6)	Diverse	Diverse	Single indiv. reprod.	Diverse
Attachment (variable 12)	None–firm	None–*firm*	Firm	None
Body flexibility (variable 13)	Inflexible–flexible	Inflexible–flexible	Flexible	Inflexible–flexible
Body form (variable 14)	Diverse	Streamlined–flattened	Streamlined–flattened	Diverse
Mobility (l) (variable 10)	Immobile–mobile	Relatively mobile	Mobile	Relatively immobile
Resistant stages (variable 15)	Absent–present	Absent–present‡	Present	Absent–present§

* Derived from variables 3, 4, 5, and 15.
† Derived from variables 3 and 5.
‡ Embryonic.
§ Imaginal.

Caenidae or Baetidae). Furthermore, the average size of organisms (variable 1) is assumed to decrease in temporally unstable habitats (Townsend & Hildrew, 1994). However, there is no clear relation between temporal variability and the potential size of individuals (Fig. 9) for the Insecta, partly because of the presence of large-sized species of Odonata and Coleoptera (Dytiscidae) at high temporal variability (Fig. 8b). These taxa, which have specific behavioural or physiological adaptations (aerial larval respiration, vertical migrations), can survive in adverse conditions.

In the Upper Rhône, the lowest temporal and spatial variability occurs in the main channel (EUmaS, EUacS, Fig. 8a). As underscored by the predictions developed by Townsend & Hildrew (1994), this relative stability favours the development of taxa with long-lived aquatic stages (Fig. 9, variable 3). However, a consequence of having a longer development time at low frequency of disturbance is an increased risk of mortality from a longer exposure to potential competition or predation. Species may have evolved to compensate for this low theoretical rate of survivorship by a higher individual fecundity (variable 2), and this has already been observed in similar situations (Smith, Sibly & Mellor, 1987).

Furthermore, observed trends for some morphological or behavioural traits in the Insecta are opposite those predicted by Townsend & Hildrew (1994), e.g. 'attachment to soil or substrate' (variable 12), 'body flexibility' (varialble 13), or 'body form' (variable 14, Table 2). There is an explanation for this mismatch. These traits seem to be more closely linked with the abiotic characteristics of the habitat (flowing or stagnant water) than with its more or less high stability (see also Usseglio-Polatera & Tachet, 1994). Habitats exhibiting low spatial and temporal variability are lotic environments, that are assumed to have (fairly) adverse physical conditions. As a result, resident species have to 'invest' in morphological adaptations in order to resist such abiotic conditions. However, these adaptations may have a high metabolic cost (e.g. Willows, 1987) so that the extent of the species' investment into somatic growth overall will be lower. For instance, large species of Plecoptera (Perlidae, Perlodidae) have a reduced potential number of cycles per year and per individual (even if their individual fecundity is rather high for the reasons described above). Many of them have evolved adult brachyptery varying from a small reduction in wing length to the absence of wings. One likely explanation is that there is an advantage conferred

by using the energy necessary for wing production in other somatic investments or in reproductive products (see Brittain, 1990).

It is assumed that species' dissemination abilities increase their ability to colonize refugia or disturbed patches (Townsend, 1989). The observed decrease in larval dissemination abilities along a gradient of increasing spatial variability (Fig. 9, variable 10) implies that mobility and refugial abundance are inversely related in aquatic Insecta. In addition, unfavourable conditions (high summer temperatures and droughts) may be avoided by embryonic or larval dormancy (e.g. Iversen *et al.*, 1978; Brittain, 1982; Canton *et al.*, 1984; Sephton & Hynes, 1984; Pugsley & Hynes, 1985; Brittain, 1990). As emphasized by Tauber, Tauber & Masaki, (1986), Southwood (1988), and Brittain (1990), this diapause has a double advantage: (i) it allows an individual to withstand a harsh period with minimal metabolic costs; and (ii) it ensures high synchronicity among growth, reproduction, and optimal abiotic conditions. This double advantage may be the reason for the occurrence of embryonic and larval diapause in habitat types that differ considerably in summer temperatures and risk of droughts (e.g. the main channel and temporary waters). The more or less short aerial adult stage is assumed to be another critical phase in the life cycle of aquatic insects. However, copulation is not always necessary because parthenogenesis is relatively frequent (Fig. 9, variable 6). The adults of insects in habitats with high temporal variability are long lived, sometimes with a period of dormancy (Fig. 9, variables 5 and 15), which allows them to survive drought periods (Novak & Sehnal, 1963; Malicky, 1981) and supports the predictions of Townsend & Hildrew (1994) on the occurrence of invulnerable life stages at such conditions.

It appears that an insect species' ability to participate in the more or less frequent recolonization of habitats after disturbances is based on their phylogenetic history. The clear discrimination between Plecoptera, Ephemeroptera, Odonata, Trichoptera, and Coleoptera on the factorial plane F1 × F2 of the species trait analysis (Fig. 1b), as well as the results of the co-inertia analysis (Fig. 7), indicate that the selected traits are rather similar for a given order. Most orders (apart from Plecoptera) contain species (or species groups, such as the Coleoptera) with similar species traits but very different spatial dis-

tributions (Fig. 7). Therefore, it can be argued that species traits that were not considered in this study (because not enough information was available for them) may play an important role in the distribution of the aquatic Insecta.

Species richness and spatial—temporal habitat variability

According to Townsend's (1989) patch dynamics concept, and the predictions of Townsend & Hildrew (1994), species richness is expected to peak at intermediate levels of temporal variation and to increase with spatial heterogeneity. These predictions on species richness are not observed along the axis of spatial heterogeneity (Fig. 10). The highest species richness is observed in paleopotamic habitats that have an intermediate temporal variability when compared with all twenty-two habitat types (see Cellot *et al.*, 1994). This is the consequence of the high number of Coleoptera species in paleopotamic habitats (see Richoux, 1994), Comparison of the species richness of habitat types with low spatial variability that are ordered along the axis of temporal variability (from EUacS/EUmaS to EUbpS in Fig. 10) reveals no trend. As a consequence, predictions on patterns of species richness (at the community level) are not confirmed by observations on these five aquatic insect orders in the Upper Rhône.

Conclusions

At the two sites examined in the Upper Rhône, habitat utilization is obviously related to species traits, but it appears that many species traits encountered do not conform with trends derived from the river habitat templet. However, reasonable explanations can be found for many of the deviations of observations from predictions. For example, it is likely that for the fecundity, the number of cycles per individual, and the life cycle duration, a major trade-off is between producing many offspring on a single occasion (= semelparity) and producing a few offspring each time over on a series of breeding seasons (= iteroparity). The former tactic has evolved in Plecoptera, Ephemeroptera, Odonata, and Trichoptera; the latter has evolved in the Coleoptera. Moreover, morphological and behavioural attributes observed stable main channel habitats result from selection

that is predominantly related to flow. In contrast, stagnant water may be colonized by taxa having a variety of body shapes, especially in the Coleoptera. This order exhibits a relatively high morphological diversity and certainly the highest diversity in physiological adaptations; in addition, Coleoptera have a set of homogeneous species traits adapted to events such as desiccation or food absence, which partially releases them from many of the constraints in the aquatic environment (Richoux, 1994).

As emphasized by Southwood (1988, p. 10), 'what is evolved in a given organism will depend on the constraints on its morphology and physiology arising from its phylogenetic history'. In this context, it is quite obvious that the Coleoptera display an original situation. In contrast to the Plecoptera, Ephemeroptera, Odonata, and Trichoptera, the Coleoptera are not primary invaders of the aquatic environment. As a result, they did not have to solve the same set of biological problems in their evolution, and subsequently deviate in their adaptative solutions in responses to a particular environmental situation.

Acknowledgments

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Appendix 1 Number and name of Odonata species collected in the Rhône River and its alluvial floodplain habitats at Brégnier-Cordon and Jons, and considered in this analysis. For the species list of the other four insect orders considered in this paper, see Richoux (1994), Tachet *et al.* (1994), and Usseglio-Polatera & Tachet (1994)

Family Calopterygidae
  1 *Calopteryx splendenx* (Harris)
Family Lestidae
  2 *Chalcolestes viridis* (Van der Linden)
Family Platycnemidae
  3 *Platycnemis pennipes* (Pallas)
Family Coenagrionidae
  4 *Pyrrhosoma nymphula* (Sulzer)
  5 *Ischnura elegans* (Van der Linden)
  6 *Coenagrion mercuriale* (Charpentier)
  7 *C. puella* (L.)
  8 *Enallagma cyathigerum* (Charpentier)
  9 *Erythromma najas* (Hansemann)
10 *E. viridulum* (Charpentier)
Family Aeshnidae
11 *Anax imperator* Leach
Family Libellulidae
12 *Ladona fulva* Müller
13 *Crocothemis erythraea* (Brulle)
14 *Sympetrum striolatum* (Charpentier)

Appendix 2   Species traits (Var.) and modalities (Mod.) of Odonata used in this analysis (Castella, personal communication; see Table 1 for numbers of variables and modalities and Appendix 1 for number of species). For the other four insect orders considered in this paper, this matrix was completed by modifying the appendices of Richoux (1994), Tachet *et al.* (1994), and Usseglio-Polatera & Tachet (1994)

Var.	Mod.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	4	1	1	3	3	3	3	3	3	3	3	0	0	3	3
	5	3	3	0	0	0	0	0	0	0	0	3	3	1	0
2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	1	0	0	0	0	0	0	0	0	0	0	1	3	0	0
	2	3	3	3	3	3	3	3	3	3	3	3	0	3	3
	3	0	0	0	0	1	0	0	0	0	0	0	0	1	0
	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	1	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	3	3	3	3	3	3	3	3	3	3	3	0	3	3	3
	4	3	3	0	3	3	3	3	3	3	3	3	3	3	3
	5	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3
7	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0
	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	3	0	0	0	2	2	0	1	0	0	0	0	1	0	0
	4	2	0	2	2	2	2	2	2	2	1	2	2	2	1
	5	3	1	2	3	2	2	3	2	2	2	2	3	2	2
	6	3	2	3	0	3	3	3	3	3	3	3	0	3	3
	7	2	3	3	0	3	0	1	3	1	1	2	0	2	3
	8	0	2	0	0	2	0	0	1	0	0	0	0	0	3
	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	1	0	0	0	0	0	0	0	0	0	0	0	2	2	3
	2	3	3	3	3	3	3	3	3	3	3	3	0	0	0
	3	0	0	0	0	0	0	0	0	0	0	0	1	1	0
	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	1	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2	1	1	1	1	1	1	1	1	1	1	0	0	0	0
	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	4	1	1	1	1	1	1	1	1	1	1	3	3	3	3
	5	0	0	0	0	0	0	0	0	0	0	1	1	2	2
12	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0	0	3	3	3	3
	3	3	3	3	3	3	3	3	3	3	3	2	0	0	0
14	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1
	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	1	3	1	3	3	3	3	3	3	3	3	3	3	3	3
	2	0	3	0	0	0	0	0	0	0	0	1	0	1	1
	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	1	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	7	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	8	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	9	3	3	3	3	3	3	3	3	3	3	3	3	3	3
18	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0	0	0	3	0	0	0
	6	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	7	3	3	3	3	3	3	3	3	3	3	1	3	3	3
	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	4	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0