

Problème Pratique de Statistique - 29

Traits biologiques et écologiques des insectes aquatiques

L'usage du codage flou dans l'enregistrement des traits biologiques est illustré par deux tableaux importants dus à B. Statzner et son équipe. Comment mesurer la redondance dans ce type d'information ?

Avec `data(bseta197)` dans la librairie `ade4`, on obtient une copie d'un jeu de données important publié par Statzner et al. (1997).

Les données sont présentées sous la forme de deux tableaux de variables floues. Chaque ligne est une espèce. Les colonnes sont des modalités regroupées par variables. Par exemple le taxon 43 (*Ephemera vulgata* L., EPHEMEROPTERA, Ephemeridae) pour le trait biologique "taille des femelles" présente le profil :

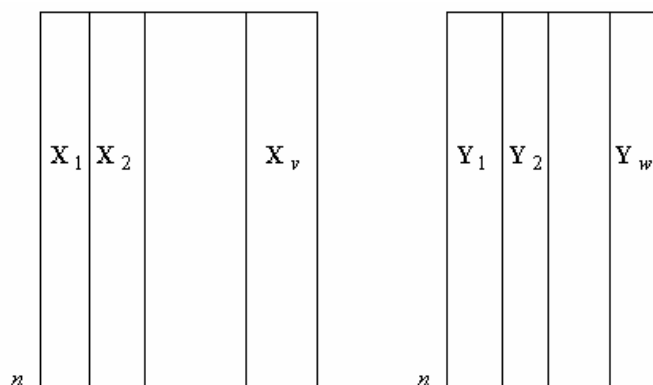
$$\begin{array}{ccccccc} 1 & 2 & 3 & 4 & 5 & 6 & 7 \\ [0 & 0 & 2 & 2 & 0 & 0 & 0] \end{array}$$

Ceci signifie que cette taille est dans la classe]10 mm, 15 mm] dans 50% des cas et dans la classe]15 mm, 20 mm] dans les autres cas. Le premier tableau est formé de la juxtaposition de 10 traits biologiques comptant au total 41 modalités.

Dans le second tableau, à la ligne 43 on trouve pour le trait écologique "lieu de ponte" le profil :

$$\begin{array}{ccccccc} 1 & 2 & 3 & 4 & 5 & 6 & 7 \\ [0 & 1 & 2 & 0 & 0 & 0 & 0] \end{array}$$

Ceci signifie que l'espèce dépose ses œufs une fois sur trois à la surface d'une eau stagnante et deux fois sur trois à la surface d'une eau peu courante. Ce codage de l'information résulte d'une expertise des écologues basée sur une exploitation massive de la littérature naturaliste (Bournaud et al. 1992, Statzner et al. 1997, Usseglio-Polatera et al. 2000). Le premier tableau est formé de la juxtaposition de 7 traits écologiques comptant au total 34 modalités. Il y a 131 espèces d'insectes aquatiques ainsi décrites et une structure de données du type :



Le sommaire de l'article indique :

1. Using world-wide data on the reproductive biology of 131 species (in eight orders) of aquatic insects, we used multivariate analyses to examine: (i) relationships among reproductive traits determining life cycle, fecundity, morphology, behaviour and physiology; (ii) relationships among traits determining spatial and temporal habitat characteristics at different scales; and (iii) the relationship between reproductive and habitat-use traits. This provided a test of predictions of the habitat templet concept on trends of species traits along gradients of habitat heterogeneity.

2. The major trends observed in the relationships among reproductive traits were that larger females had larger eggs, which were more vulnerable to perturbations such as droughts and often laid in cocoons. In addition, they laid the eggs in larger numbers of smaller clutches than smaller females. Other traits (e.g. egg number or incubation time) did not show clear trends.

3. Females that deposited eggs at sites of low local temporal heterogeneity (within plants) used, at the same time, gross habitats of high temporal heterogeneity (temporary waters). In contrast, traits in habitat use did hardly differ along well-known gradients of temporal heterogeneity along running waters (from source to estuary). The number of habitat units used by ovipositing females generally increased with the spatial scale considered, i.e. most species oviposited in a single small habitat unit but in several gross habitats.

4. A significant ($P < 0.01$) relationship between traits in reproduction and habitat use demonstrated that habitat acted as a templet for reproductive strategies. This relationship was dominated by larger females having larger, unattached eggs which were more vulnerable to droughts and were oviposited in temporally more stable small-scale habitats (within wood or macrophytes, or within cocoons spun by the female) but more unstable large-scale habitats (primarily temporary waters). Thus, only on the small habitat scale did some of our observations correspond to the predictions of the habitat templet concept (e.g. larger size or higher vulnerability in more stable habitats). However, many species had traits in reproduction that did not show trends as predicted by the concept.

5. This and other recent studies of the relationships between traits of freshwater organisms and the heterogeneity of their habitats have shown that habitat acts as a templet for species life history traits. However, many of the details observed in these studies did not correspond to predictions of the templet concept because of trade-offs among the traits and scale problems in the description of habitat heterogeneity. Therefore, future studies should focus on groups of organisms that are as similar as possible in the trade-offs among their species traits and on the potential relationships of habitat heterogeneity across multiple scales.

La liste comporte 8 composantes :

species.names, **taxo**,
biol, **biol.blo**, **biol.blo.names**,
ecol, **ecol.blo** et **ecol.blo.names**.

Les deux premières contiennent l'information taxonomique des espèces concernées :

	gen	fam	ord
Acilius sulcatus	Acilius	Dytiscidae	COLEOPTERA
Agabus erichsoni	Agabus	Dytiscidae	COLEOPTERA
Agabus undulatus	Agabus	Dytiscidae	COLEOPTERA
Colymbetes fuscus	Colymbetes	Dytiscidae	COLEOPTERA
Cybister lateralimarginalis	Cybister	Dytiscidae	COLEOPTERA
Dytiscus marginalis	Dytiscus	Dytiscidae	COLEOPTERA

Dytiscus semisulcatus	Dytiscus	Dytiscidae	COLEOPTERA
Elmis aenea	Elmis	Elmidae	COLEOPTERA
Stenelmis sexlineata	Stenelmis	Elmidae	COLEOPTERA
Gyrinus substriatus	Gyrinus	Gyrinidae	COLEOPTERA
Orectochilus villosus	Orectochilus	Gyrinidae	COLEOPTERA
Enochrus quadripunctatus	Enochrus	Hydrophilidae	COLEOPTERA
Hydrobius fuscipes	Hydrobius	Hydrophilidae	COLEOPTERA
Hydrochara caraboides	Hydrochara	Hydrophilidae	COLEOPTERA
Hydrophilus piceus	Hydrophilus	Hydrophilidae	COLEOPTERA
Hydrophilus triangularis	Hydrophilus	Hydrophilidae	COLEOPTERA
Psephenus falli	Psephenus	Psephenidae	COLEOPTERA
Psephenus herricki	Psephenus	Psephenidae	COLEOPTERA
Chironomus plumosus	Chironomus	Chironomidae	DIPTERA
Culex pipiens	Culex	Culicidae	DIPTERA
Boopthora erythrocephala	Boopthora	Simuliidae	DIPTERA
Eusimuliu aureum	Eusimuliu	Simuliidae	DIPTERA
Odagmia ornata	Odagmia	Simuliidae	DIPTERA
Simulium morsitans	Simulium	Simuliidae	DIPTERA
Simulium noelleri	Simulium	Simuliidae	DIPTERA
Simulium vittatum	Simulium	Simuliidae	DIPTERA
Wilhelmia equina	Wilhelmia	Simuliidae	DIPTERA
Wilhelmia lineata	Wilhelmia	Simuliidae	DIPTERA
Lipsothrix nigrilinea	Lipsothrix	Tipulidae	DIPTERA
Tipula sacra	Tipula	Tipulidae	DIPTERA
Baetis fuscatus	Baetis	Baetidae	EPHEMEROPTERA
Baetis rhodani	Baetis	Baetidae	EPHEMEROPTERA
Callibaetis floridanus	Callibaetis	Baetidae	EPHEMEROPTERA
Caenis horaria	Caenis	Caenidae	EPHEMEROPTERA
Caenis luctuosa	Caenis	Caenidae	EPHEMEROPTERA
Ephemerella dorothea	Ephemerella	Ephemerellidae	EPHEMEROPTERA
Ephemerella ignita	Ephemerella	Ephemerellidae	EPHEMEROPTERA
Ephemerella needhami	Ephemerella	Ephemerellidae	EPHEMEROPTERA
Ephemerella rotunda	Ephemerella	Ephemerellidae	EPHEMEROPTERA
Ephemera danica	Ephemera	Ephemeridae	EPHEMEROPTERA
Ephemera simulans	Ephemera	Ephemeridae	EPHEMEROPTERA
Ephemera varia	Ephemera	Ephemeridae	EPHEMEROPTERA
Ephemera vulgata	Ephemera	Ephemeridae	EPHEMEROPTERA
Epheron album	Epheron	Ephemeridae	EPHEMEROPTERA
Ecdyonurus forcipula	Ecdyonurus	Heptageniidae	EPHEMEROPTERA
Epeorus humeralis	Epeorus	Heptageniidae	EPHEMEROPTERA
Epeorus pleuralis	Epeorus	Heptageniidae	EPHEMEROPTERA
Heptagenia hebe	Heptagenia	Heptageniidae	EPHEMEROPTERA
Rhithrogena semicolorata	Rhithrogena	Heptageniidae	EPHEMEROPTERA
Stenonema fuscum	Stenonema	Heptageniidae	EPHEMEROPTERA
Leptophlebia cupida	Leptophlebia	Leptophlebiidae	EPHEMEROPTERA
Leptophlebia vespertina	Leptophlebia	Leptophlebiidae	EPHEMEROPTERA
Siphonurus quebecensis	Siphonurus	Siphonuridae	EPHEMEROPTERA
Orohermes crepusculus	Orohermes	Corydalidae	MEGALOPTERA
Sialis fuliginosa	Sialis	Sialidae	MEGALOPTERA
Sialis lutaria	Sialis	Sialidae	MEGALOPTERA
Sialis rotunda	Sialis	Sialidae	MEGALOPTERA
Aeshna isosceles	Aeshna	Aeshnidae	ODONATA
Anax imperator	Anax	Aeshnidae	ODONATA
Calopteryx maculata	Calopteryx	Calopterygidae	ODONATA
Phaon iridipennis	Phaon	Calopterygidae	ODONATA
Pyrrhosoma nymphula	Pyrrhosoma	Coenagrionidae	ODONATA
Epiophlebia superstes	Epiophlebia	Epiophlebiidae	ODONATA
Archilestes grandis	Archilestes	Lestidae	ODONATA
Lestes congener	Lestes	Lestidae	ODONATA
Lestes eurinus	Lestes	Lestidae	ODONATA
Lestes viridis	Lestes	Lestidae	ODONATA
Zygonyx natalensis	Zygonyx	Libellulidae	ODONATA
Platycnemis pennipes	Platycnemis	Platycnemidae	ODONATA
Osmylus fulvicephalus	Osmylus	Osmylidae	PLANIPENNIA
Sisyra fuscata	Sisyra	Sisyridae	PLANIPENNIA
Allocapnia pygmaea	Allocapnia	Capniidae	PLECOPTERA
Capnia bifrons	Capnia	Capniidae	PLECOPTERA
Alloperla onkos	Alloperla	Chloroperlidae	PLECOPTERA
Chloroperla torrentium	Chloroperla	Chloroperlidae	PLECOPTERA
Eustheniopsis venosa	Eustheniopsis	Eustheniidae	PLECOPTERA
Dinotoperla brevipennis	Dinotoperla	Gripopterygidae	PLECOPTERA
Leuctra hippopus	Leuctra	Leuctridae	PLECOPTERA
Nemoura avicularis	Nemoura	Nemouridae	PLECOPTERA
Nemoura cinerea	Nemoura	Nemouridae	PLECOPTERA
Nemoura trispinosa	Nemoura	Nemouridae	PLECOPTERA

Nemurella pictetii	Nemurella	Nemouridae	PLECOPTERA
Dinocras cephalotes	Dinocras	Perlidae	PLECOPTERA
Neoperla clymene	Neoperla	Perlidae	PLECOPTERA
Paragnetina media	Paragnetina	Perlidae	PLECOPTERA
Perla burmeisteriana	Perla	Perlidae	PLECOPTERA
Perla bipunctata	Perla	Perlidae	PLECOPTERA
Diura bicaudata	Diura	Perlodidae	PLECOPTERA
Hydroperla crosbyi	Hydroperla	Perlodidae	PLECOPTERA
Isoperla clio	Isoperla	Perlodidae	PLECOPTERA
Isoperla transmarina	Isoperla	Perlodidae	PLECOPTERA
Perlodes mortoni	Perlodes	Perlodidae	PLECOPTERA
Pteronarcys proteus	Pteronarcys	Pteronarcidae	PLECOPTERA
Taeniopteryx nebulosa	Taeniopteryx	Taeniopterygidae	PLECOPTERA
Beraeodes minutus	Beraeodes	Beraeidae	TRICHOPTERA
Brachycentrus nigrisoma	Brachycentrus	Brachycentridae	TRICHOPTERA
Brachycentrus subnubilus	Brachycentrus	Brachycentridae	TRICHOPTERA
Oligoplectrum maculatum	Oligoplectrum	Brachycentridae	TRICHOPTERA
Agapetus bifidus	Agapetus	Glossosomatidae	TRICHOPTERA
Agapetus fuscipes	Agapetus	Glossosomatidae	TRICHOPTERA
Cheumatopsyche campyla	Cheumatopsyche	Hydropsychidae	TRICHOPTERA
Cheumatopsyche lasia	Cheumatopsyche	Hydropsychidae	TRICHOPTERA
Cheumatopsyche speciosa	Cheumatopsyche	Hydropsychidae	TRICHOPTERA
Hydropsyche angustipennis	Hydropsyche	Hydropsychidae	TRICHOPTERA
Hydropsyche instabilis	Hydropsyche	Hydropsychidae	TRICHOPTERA
Hydropsyche phalerata	Hydropsyche	Hydropsychidae	TRICHOPTERA
Hydropsyche simulans	Hydropsyche	Hydropsychidae	TRICHOPTERA
Athripsodes aterrimuss	Athripsodes	Leptoceridae	TRICHOPTERA
Athripsodes cinereus	Athripsodes	Leptoceridae	TRICHOPTERA
Ceraclea senilis	Ceraclea	Leptoceridae	TRICHOPTERA
Mystacides longicornis	Mystacides	Leptoceridae	TRICHOPTERA
Oecetis lacustris	Oecetis	Leptoceridae	TRICHOPTERA
Triadenodes bicolor	Triadenodes	Leptoceridae	TRICHOPTERA
Apatania fimbriata	Apatania	Limnephilidae	TRICHOPTERA
Apatania muliebris	Apatania	Limnephilidae	TRICHOPTERA
Apatania zonella	Apatania	Limnephilidae	TRICHOPTERA
Clistoronia magnifica	Clistoronia	Limnephilidae	TRICHOPTERA
Drusus annulatus	Drusus	Limnephilidae	TRICHOPTERA
Limnephilus flavicornis	Limnephilus	Limnephilidae	TRICHOPTERA
Limnephilus lunatus	Limnephilus	Limnephilidae	TRICHOPTERA
Onocosmoecus unicolor	Onocosmoecus	Limnephilidae	TRICHOPTERA
Potamophylax latipennis	Potamophylax	Limnephilidae	TRICHOPTERA
Pseudostenophylax edwardsi	Pseudostenophylax	Limnephilidae	TRICHOPTERA
Philopotamus montanus	Philopotamus	Philopotamidae	TRICHOPTERA
Oligotricha striata	Oligotricha	Phryganeidae	TRICHOPTERA
Phryganea grandis	Phryganea	Phryganeidae	TRICHOPTERA
Neureclipsis bimaculata	Neureclipsis	Polycentropodidae	TRICHOPTERA
Plectrocnemia conspersa	Plectrocnemia	Polycentropodidae	TRICHOPTERA
Rhyacophila nubila	Rhyacophila	Rhyacophilidae	TRICHOPTERA
Notidobia ciliaris	Notidobia	Sericostomatidae	TRICHOPTERA
Sericostoma personatum	Sericostoma	Sericostomatidae	TRICHOPTERA

On pourra manipuler ce type d'information à partir de la fonction **as.taxo**.

biol est un data.frame avec 131 lignes (espèces) et 41 colonnes (modalités de traits biologiques). **biol.blo.names** donne le nom des 10 traits et **biol.blo** donne le nombre de modalités par trait soit :

Fem.Size	Egg.length	Egg.number	Generations	Oviposition
7	6	6	3	3
Incubation	Egg.shape	Egg.attach	Clutch.struc	Clutch.number
3	3	4	3	3

Les noms des variables de **biol** explicite au mieux la structure de ce type d'information avec le code donné par les auteurs :

Trait (code)	Trait (content)	No.	Code	Modality
Fem.Size	Female size	1	size.1	≤5 mm
		2	size.2	>5-10 mm
		3	size.3	>10-15 mm
		4	size.4	>15-20 mm
		5	size.5	>20-25 mm
		6	size.6	>25-30 mm
		7	size.7	>30 mm
Egg.length	Egg length	1	egglen.1	≤0.2 mm
		2	egglen.2	>0.2-0.3 mm
		3	egglen.3	>0.3-0.4 mm
		4	egglen.4	>0.4-0.5 mm
		5	egglen.5	>0.5-1.0 mm
		6	egglen.6	>1.0 mm
Egg.number	Egg number	1	eggnum.1	≤100
		2	eggnum.2	>100-300
		3	eggnum.3	>300-500
		4	eggnum.4	>500-1500
		5	eggnum.5	>1500-3000
		6	eggnum.6	>3000
Generations	Generations per year	1	genery.1	≤1
		2	genery.2	2
		3	genery.3	>2
Oviposition	Oviposition period	1	oviper.1	≤2 months
		2	oviper.2	>2-5 months
		3	oviper.3	>5 months
Incubation	Incubation time	1	incub.1	≤4 weeks
		2	incub.2	>4-12 weeks
		3	incub.3	>12 weeks
Egg.shape	Egg shape	1	esha.spher	spherical (i.e. length/width ratio ≈1)
		2	esha.oval	oval (i.e. length/width ratio >1 and <3)
		3	esha.cyli	cylindrical (i.e. length/width ratio ≥3)
Egg.attach	Egg attachment	1	eggatta.1	no attachment mechanisms
		2	eggatta.2	attachment structures on egg
		3	eggatta.3	adhesive gelatinous matrix or cement
		4	eggatta.4	cocoon or woven silk
Clutch.struc	Clutch structure	1	egg.sing	single eggs (oviposition of isolated eggs)
		2	egg.group	grouped eggs isolating after oviposition
		3	egg.mass	egg masses
Clutch.number	Clutch number	1	clunum.1	1
		2	clunum.2	2
		3	clunum.3	>2

ecol.blo.names donne le nom des 7 traits et **ecol.blo** donne le nombre de modalités par trait soit :

Oviposi_site	Substrat_eggs	Egg_deposition	Gross_habitat
7	6	4	8
Saturation	Time_day	Season	
2	4	3	

Les noms des variables de **ecol** explicite au mieux la structure de ce type d'information avec le code donné par les auteurs :

Trait (code)	Trait (content)	No.	Code	Modality
Oviposi_site	Oviposition site	1	ovisite.1	above the water
		2	ovisite.2	water surface, stagnant
		3	ovisite.3	water surface, slow current
		4	ovisite.4	water surface, fast current
		5	ovisite.5	immersed, stagnant
		6	ovisite.6	immersed, slow current
		7	ovisite.7	immersed, fast current
Substrat_eggs	Substratum type for eggs	1	eggsub.1	silt
		2	eggsub.2	sand
		3	eggsub.3	gravel and stones
		4	eggsub.4	fine-structured vegetation (algae)
		5	eggsub.5	coarse-structured vegetation (macrophytes)
		6	eggsub.6	wood
Egg_deposition	Egg deposition	1	eggdep.1	free from substratum
		2	eggdep.2	on substratum
		3	eggdep.3	underneath substratum
		4	eggdep.4	within substratum
Gross_habitat	Gross habitat	1	habitat.1	freshwater in general, no specialisation
		2	habitat.2	sources
		3	habitat.3	headwaters and small streams
		4	habitat.4	lower reaches and large rivers
		5	habitat.5	lakes (stagnant waters in general)
		6	habitat.6	temporary waters, puddles, ponds
		7	habitat.7	brackish waters, estuaries
		8	habitat.8	swamps
Saturation	Saturation variance	1	satur.perm	permanent water saturation
		2	satur.temp	temporary water saturation
Time_day	Time of day	1	time.morn	morning
		2	time.day	day
		3	time.even	evening
		4	time.night	night
Season	Season	1	spring	spring (April-June)
		2	summer	summer (July-September)
		3	autumn	autumn (October-December)

Ce type de données pose nombre de questions originales : comment mesurer la corrélation entre deux traits, comment mesurer la cohérence entre plusieurs traits, comment tester l'influence de la taxonomie sur chaque trait, chaque bloc de traits, comment mesurer le lien entre les deux types d'information ? Ce lien est-il important ou n'est-il qu'une trace de l'histoire évolutive des espèces ? Aucune de ces questions n'est simple.

- Bournaud, M., P. Richoux, and P. Usseglio-Polatera. 1992. An approach to the synthesis of qualitative ecological information from aquatic coleoptera communities. *Regulated rivers: Research and Management* **7**:165-180.
- Statzner, B., K. Hoppenhaus, M.-F. Arens, and P. Richoux. 1997. Reproductive traits, habitat use and templet theory: a synthesis of world-wide data on aquatic insects. *Freshwater Biology* **38**:109-135.
- Usseglio-Polatera, P., M. Bournaud, P. Richoux, and H. Tachet 2000. Biomonitoring through biological traits of benthic macroinvertebrates: how to use species trait databases? *Hydrobiologia* **422-423**:153-162.