Do mediterranean genera not included in Tachet *et al.* 2002 have mediterranean trait characteristics?

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ABSTRACT

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Multiple-trait databases are increasingly used in community ecology in different regions of the world. In Europe, Tachet *et al.* (2002) compiled an aquatic macroinvertebrate database for 473 taxa using information on 11 biological traits described by 63 categories. However, less studied regions, at the time of the compilation of the database, such as the mediterranean Basin, can harbour exclusive genera, which were not included in Tachet's database. In a large-scale study across the mediterranean Basin, we found 44 genera that were not included in Tachet's database (NEW genera). Our main aim was to compile trait information for these NEW genera and assess whether these genera had specific traits that could explain their exclusivity to the Mediterranean region. We compared the trait characteristics of NEW genera to those of genera only found in Mediterranean or temperate regions that were included in the Tachet's database (MED and TEM genera, respectively). We found that NEW genera had more mediterranean characteristics than TEM genera and that some trait categories of NEW genera were even more mediterranean-like than the traits of MED genera (e.g., diapause). Therefore, our results suggest that the specific biological traits of these NEW genera allow them to cope successfully and exclusively with the harsh environmental conditions of the mediterranean climate rivers, which could partially explain their absence in Tachet's database. Other explanations, such as the limited dispersal ability of these NEW genera to reach and colonize temperate Europe or the rarity of these NEW genera, should also be considered. We provide biological traits of the NEW genera to be used in future studies on the mediterranean river ecology.

Key words: Aquatic macroinvertebrates, biological traits, fuzzy coding, Mediterranean Basin, temperate Europe.

RESUMEN

¿Los géneros mediterráneos no incluidos en la Tachet et al. (2002) presentan rasgos típicamente mediterráneos?

Las bases de datos de múltiples rasgos biológicos están siendo cada vez más utilizadas en ecología de comunidades en distintas regiones del mundo. En Europa, Tachet et al. (2002) recopilaron información de macroinvertebrados acuáticos para 473 taxones de 11 rasgos biológicos que incluyen 63 categorías. No obstante, es esperable que las regiones menos estudiadas durante la recopilación de datos, tales como las mediterráneas, alberguen géneros exclusivos que por falta de información no fueron incluidos inicialmente en la base de datos de Tachet. En un estudio a lo largo de la cuenca mediterránea, se encontraron 44 géneros no incluidos en la base de datos de Tachet (géneros NEW). Nuestro principal objetivo fue recoger información de estos géneros y analizar si tenían rasgos mediterráneos específicos que pudieran explicar su exclusividad en estos ambientes. Así, comparamos los rasgos de los géneros NEW con aquellos géneros encontrados en las regiones mediterráneas y templadas incluidos en la base de datos de Tachet (géneros MED y TEM, respectivamente). Los resultados mostraron que los géneros NEW tenían rasgos más mediterráneos que los géneros TEM, y que algunos de ellos incluso lo eran más que los de los géneros MED (e.g. diapausa). Por lo tanto, nuestros resultados sugieren que los rasgos específicos de estos géneros NEW les permiten hacer frente a las condiciones ambientales que caracterizan los ríos mediterráneos, lo que podría explicar, en parte, su ausencia en la base de datos de Tachet. Asimismo, se han considerado otras razones, tales como

la limitada dispersión de estos géneros NEW para colonizar la Europa templada o su rareza. Se proporcionan los rasgos biológicos de estos géneros NEW para ser utilizados en futuros estudios en ríos de clima mediterráneo.

Palabras clave: *Macroinvertebrados acuáticos, rasgos biológicos, codificación difusa, cuenca mediterránea, Europa templada.*

INTRODUCTION

Biological traits are individual attributes that determine the presence of species in particular habitats and the ability of species to interact with other species. Considered both a product of the ecology (sorting) and the evolutionary history of species, traits have been utilised in many fields, including community ecology, molecular phylogenetics and biodiversity conservation (Statzner *et al.*, 2001; Macleod & Forey, 2002; Cavender-Bares *et al.*, 2004; Henry *et al.*, 2008). Multiple-trait databases are available for a wide variety of taxa, although plants are clearly the organisms that have had more attention (Kühn *et al.*, 2004). For freshwater macroinvertebrates, there are currently five main databases that include many genera present in Europe (Tachet *et al.*, 2002), North America (Bêche *et al.*, 2006; Vieira *et al.*, 2006), South-America (Tomanova & Usseglio-Polatera, 2007) and New Zealand (Dolédec *et al.*, 2006). Studies dealing with these databases have analysed trait responses to several environmental gradients, including natural disturbance, pollution, and hydrological or latitudinal aspects (Statzner *et al.*, 2005; Bêche *et al.*, 2006; Bonada *et al.*, 2007b; Horrigan & Baird, 2008). Scientists agree that the use of traits offers a great opportunity to understand how the functional role of freshwater macroinvertebrate communities is constrained by the environment.

For France, Belgium and Pyrénées, the database of Tachet *et al.* (hereafter Tachet's database) specifically comprises 11 biological traits and 63 categories that consider aspects related to the morphology, behaviour, life history and physiology of freshwater macroinvertebrates (Table 1) alongside 11 ecological traits that are described by 60 categories. For each taxon, these authors coded each trait category using a fuzzy coding approach (Chevenet *et al.*, 1994), where a value of 0 indicates no affinity of the taxon for the trait category, 1 indicates low affinity, 2 indicates medium affinity and 3 or > 3 indicates strong affinity. In contrast to a presence/absence approach, fuzzy coding provides semi-quantitative data and considers trait plasticity within genera or across space (i.e., a multivoltine species in the Mediterranean Basin can be semivoltine in Scandinavia). Tachet's database incorporates 473 taxa, mostly at the genus level (433), and the authors used information gathered from ~ 6000 published and unpublished studies. These studies cover a time period of more than one century – the first record in Tachet's database dates back to 1802 – and include all information collected in Europe until the publication of the database. Therefore, even though it only includes French, Belgium and Pyrenean genera, Tachet's database considers the expression of invertebrate biological traits from many European regions. However, exclusive genera from other European countries may not be present in the Tachet's database, and their biological traits need to be coded for better characterization of the functional characteristics in these countries.

Studying large scale responses of freshwater macroinvertebrates traits to natural disturbance, Statzner *et al.* (2007) and Bonada *et al.* (2007a; unpublished material) found several genera present in the Mediterranean Basin that were not included in the Tachet's database. Considering the increasing use of macroinvertebrate traits in freshwater studies, our main aim was to code these genera in a similar way as in Tachet's database and to make this information

Table 1. Genus biological traits and categories from Tachet *et al.* (2002) with their associated codes. Predictions indicate whether the category proportion should be higher in the mediterranean than in the temperate region (M) or the contrary (T). The rationale behind each prediction can be found in Bonada *et al.* (2007). *Géneros y categorías biológicas utilizadas en Tachet* et al. *(2002) con los correspondientes códigos. Las predictiones indican si la categoría debería tener una mayor proporción en la región mediterránea que en la templada (M) o lo contrario (T). La razón de cada predicción se describe en Bonada* et al. *(2007).*

Trait	Category	Code	Predictions
Maximal size	≤ 0.25 cm	a1	M
	> 0.25 − 0.5 cm	a2	M
	> 0.5 − 1 cm	a3	T
	> 1 − 2 cm	a4	T
	> 2 − 4 cm	a5	M
	> 4 − 8 cm	a6	M
	> 8 cm	a7	
Life cycle duration	≤ 1 year	b1	M
	> 1 year	b2	
Potential number of reproduction cycles per year	< 1	c1	T
	1	c2	
	> 1	c3	
Aquatic stages	egg	d1	
	larva	d2	T
	nymph	d3	
	imago	d4	M
Reproduction	Ovoviviparity	e1	M
	Isolated eggs, free	e2	
	Isolated eggs, cemented	e3	
	Clutches, cemented or fixed	e4	
	Clutches, free	e5	
	Clutches in vegetation (endophytic)	e6	
	Clutches, terrestrial	e7	M
	Asexual reproduction	e8	M
Dissemination	Aquatic passive	f1	T
	Aquatic active	f2	
	Aerial passive	f3	
	Aerial active	f4	M
Resistance forms	Eggs, statoblasts, gemmules	g1	
	Cocoons	g2	
	Cells against desiccation	g3	M
	Diapause or dormancy	g4	M
	None	g5	T
Respiration	Tegument	j1	
	Gill	j2	M
	Plastron	j3	M
	Spiracle (aerial)	j4	M
Locomotion and substrate relation	Flier	u1	M
	Surface swimmer	u2	M
	Swimmer	u3	M
	Crawler	u4	T
	Burrower (epibenthic)	u5	
	Interstitial (endobenthic)	u6	M
	Temporarily attached	u7	
	Permanently attached	u8	

Cont.

Table 1. *cont.*

Trait	Category	Code	Predictions
Food	Fine sediment + micrographisms	h1	
	Detritus < 1 mm	h2	
	Plant detritus ≥ 1 mm	h3	T
	Living microphytes	h4	M
	Living macrophytes	h5	M
	Dead animal > 1 mm	h6	
	Living microinvertebrates	h7	
	Living macroinvertebrates	h8	
	Vertebrates	h9	
Feeding habits	Deposit feeder	i2	
	Shredder	i3	T
	Scraper	i4	M
	Filter-feeder	i5	
	Piercer (plant or animal)	i6	
	Predator (carver/engulfer/swallower)	i7	
	Parasite, parasitoid	i8	

available to future trait studies in Mediterranean Basin rivers. We further assessed whether the absence of these mediterranean genera in temperate Europe, and therefore in Tachet's database, resulted from mediterranean-specific traits that did not match temperate conditions (Bonada *et al.*, 2007a). Therefore, we performed trait comparisons of non-coded genera in Tachet's database (NEW genera) with exclusive genera found in mediterranean and temperate regions that were included in Tachet's database (MED and TEM genera, respectively). We made this analysis based on *a priori* hypotheses about which trait categories should be highly represented in mediterranean or in temperate regions (Table 1). The rationale behind each hypothesis mainly relates to the ability of mediterranean organisms to resist or recover from summer drought and are detailed in Bonada *et al.* (2007a). Thus, we hypothesized that trait categories of NEW genera should have no significant differences with MED genera and that if significant differences were found, NEW genera should have trait categories associated with mediterranean conditions. Likewise, we also hypothesized that NEW and MED genera should differ from TEM genera in a similar way (i.e., significant differences between MED and TEM genera and between NEW and TEM genera would follow similar trends to those predicted in Table 1).

Alternatively, if NEW genera do not have characteristic mediterranean traits, other factors such as zoogeography, limited dissemination ability to reach and colonize temperate Europe, or rarity could explain their absence in Tachet's database.

MATERIAL AND METHODS

NEW genera were detected by an analysis of data from 488 sites from several studies carried out in a vast Mediterranean Basin area: from Portugal to Turkey and from France to Morocco (Statzner *et al.*, 2007; Bonada *et al.*, 2007a, unpublished material). For Dipterans, we only considered those families with some genera included in Tachet's database or Dipteran families that were not included in the database but that we found biological information for genera. For these NEW genera, we used a fuzzy coding approach similar to the approach utilised in Tachet's database. We mainly used affinity scores from 0 to 3; although for precision, scores higher than 3 (as much as 5) could be used for those traits with many categories (i.e., locomotion and substrate relation and food; Tachet *et al.*, 2002). We obtained biological information for each genus by searching through published and unpublished studies, and in a few cases, we consulted taxonomic specialists from several Mediterranean Basin coun-

tries. We found about 80 references (available upon request) that contained useful information for trait coding of our NEW genera. We gave special attention to gathering information for the known species of each genus in order to have a wider view of genus trait plasticity. When information was not available, we scored each genus as the mean of the corresponding family scores or utilised affinity scores of a closely related taxon. In these cases, we only used the information of those genera present in at least one Mediterranean Basin country according to the Fauna Europaea Web Service (2004). For example, we used the mean of Heptageniidae genera as a surrogate for the affinity scores of *Afronurus*; we used the mean of Oligoneuriidae genera as a surrogate for the affinity scores of *Isonychia* because their larvae are similar to those of Oligoneuriidae, except for maximal size (Tachet *et al.*, 2002). We assumed that traits at the family level were not biased because biological trait patterns are only minimally influenced by taxonomical resolution (Dolédec *et al.*, 2000; Gayraud *et al.*, 2003). In a few cases, we found no information on the family or on the closest taxon; we coded these trait categories as 0.

MED genera were obtained from a database of 488 sites in the Mediterranean Basin, and TEM genera were obtained from a database of 344 sites distributed across temperate Europe. Our database has the same structure as the database described in Statzner et al. (2007) and includes all of their sites and a few others from the Mediterranean Basin. The MED and TEM databases comprised 272 and 226 genera, respectively. However, from them, we only used the exclusive genera in each database (i.e., genera present in one region but not in the other) because common genera would provide redundant information. We used fuzzy correspondence analysis (FCA; Chevenet *et al.*, 1994) to compare the overall trait profile of MED, TEM and NEW genera. We assessed overall differences among groups of genera with a between-class analysis, a particular type of constrained multivariate analysis (see Dolédec & Chessel, 1989; Lebreton *et al.*, 1991). The significance of the overall difference among groups of genera (among-class variance)

was tested against simulated values obtained after 999 permutations of the rows of the trait-composition table. For each individual trait category for which we had *a priori* hypotheses, we applied Kruskal-Wallis rank sum tests for significant differences between NEW and MED/TEM genera. We used R freeware (R Development Core Team, 2010) and ade4 library (Thioulouse *et al.*, 1997; Chessel *et al.*, 2004) to perform all statistical analyses.

RESULTS

We found 44 NEW genera and obtained 77 MED and 31 TEM genera exclusive to a particular region. Of the NEW genera, 10 belonged to Prosobranchia, and 6 belonged to Odonata and Coleoptera each. The rest of the NEW genera were distributed among Hirudinoidea, Pulmonata, Crustacea, Ephemeroptera, Plecoptera, Heteroptera, and Diptera (Table 2). We found more NEW genera in Spain (19 NEW taxa) and Morocco (12 NEW taxa). However, we also had more records from these regions (169 and 91 sites, respectively) than from any other. Interestingly, we found relatively more NEW genera in Lebanon and Israel compared with the number of records used (9 genera in 18 sites in Lebanon and 6 genera in 9 sites in Israel), but the 77 records used in south France only had 5 NEW genera.

We were able to provide complete and exclusive trait information (i.e., genera with all traits X-marked in Table 2) for only 9 NEW genera, whereas 18 genera were partly coded. We did not find exclusive biological information for 17 genera; we coded them using the mean of each corresponding family or the closest taxon (Table 2). For the genus *Ochterus*, belonging to the single-genus family Ochteridae, we were only able to provide information on the "maximal size". Fuzzy-coding values for all of these non-coded genera are available in Table 3.

Overall, low but significant differences were found between MED, TEM and NEW (3.8 % of variability; simulated $P = 0.001$). The first between-class FCA axis, which explained 64 % of the trait variability, separated TEM from MED

Table 2. List of genera not included in Tachet *et al.* (2002) but present in mediterranean river surveys. All of these genera were coded by us using literature (X) or as family mean or according to a closely related taxon (=). For some traits and genera, we found no information on the genus or family (0). Country indicates the place where genera were recorded (AL for Algeria, CR for Croatia, FR for France, GR for Greece, IT for Italy, IS for Israel, LE for Lebanon, MO for Morocco, PO for Portugal, SP for Spain and TU for Turkey). *Listado de géneros no incluidos en Tachet* et al. *(2002) pero presentes en muestreos de ríos mediterráneos. Todos los géneros fueron codificados por nosotros utilizando la literatura existente (X) o el promedio de la familia correspondiente o de un taxón relacionado (=). Para algunos rasgos y géneros no se encontró información disponible para el género o su família (0). "Country" indica el país donde se encontraron los géneros (AL para Argelia, CR para Croacia, FR para Francia, GR para Grecia, IT para Italia, IS para Israel, LE para Líbano, MO para Marruecos, PO para Portugal, SP para España y TU para Turquía).*

Group	Family	Genus	Maximal size	Life cycle duration	Potential number of reproduction cycles per year	Aquatic stages	Reproduction	Dissemination	Resistance forms	Respiration	Locomotion and substrate relation	Food	Feeding habits	Comments	Country
Hirudinoidea	Hirudidae	*Limnatis*	=	=	=	=	=	=	=	=	=	=	=	Coded as mean of Hirudidae	SP
Prosobranchia	Hydrobiidae	*Belgrandiella*	=	=	=	=	=	=	=	=	=	=	=	Coded as mean of Hydrobiidae	AL
	Hydrobiidae	*Mercuria*	X	X	X	X	X	X	X	X	X	X	X		MO, SP
	Hydrobiidae	*Pseudamnicola*	X	X	X	X	X	X	X	X	X	X	X		AL, GR, MO, SP
	Hydrobiidae	*Sadleriana*	=	=	X	X	X	=	=	=	=	=	=	Coded as mean of Hydrobiidae	AL
	Hydrobiidae	*Semisalsa*	=	=	=	=	=	=	=	=	=	=	=	Coded as mean of Hydrobiidae	IS, LE
	Hydrobiidae	*Syrofontana*	=	=	=	=	=	=	=	=	=	=	=	Coded as mean of Hydrobiidae	LE
	Melanopsidae	*Fagotia*	=	=	=	=	=	=	=	=	=	=	=	Coded as *Melanopsis*	CR
	Melanopsidae	*Melanopsis*	X	X	X	X	X	X	X	X	X	X	X		IS, LE, MO, SP, TU
	Pleuroceridae	*Amphimelania*	X	0	0	=	X	=	=	=	=	=	=	Coded as mean of Thiaridae	TU
	Thiaridae	*Melanoides*	X	0	0	X	X	X	X	X	X	X	X		MO
Pulmonata	Planorbidae	*Bulinus*	X	X	X	X	X	X	X	X	X	X	X		MO
	Succineidae	*Succinea*	X	=	=	=	=	=	=	=	=	=	=	Coded as mean of Lymnaeidae	MO, TU
Crustacea	Metacrangonyctidae	*Metacrangonyx*	X	X	X	X	X	X	X	X	X	X	X	Coded using information of the family	MO
	Palaemonidae	*Palaemon*	=	=	=	=	=	=	=	=	=	=	=	Coded as *Palaemonetes*	IS
	Palaemonidae	*Palaemonetes*	X	X	X	X	X	X	X	X	X	X	X		IT, TU
Ephemeroptera	Baetidae	*Centroptiloides*	=	=	=	=	=	=	=	=	=	=	=	Coded as mean of Baetidae	GR
	Baetidae	*Nigrobaetis*	=	=	=	=	=	=	=	=	=	=	=	Coded as mean of Baetidae	SP
	Heptageniidae	*Afronurus*	=	=	=	=	=	=	=	=	=	=	=	Coded as mean of Heptageniidae	IS
	Isonychiidae	*Isonychia*	X	=	=	=	=	=	=	=	=	=	=	Coded as mean of Oligoneuriidae	TU
	Oligoneuriidae	*Oligoneuriopsis*	X	X	X	X	=	=	=	X	X	=	=	Coded as mean of Oligoneuriidae	LE, MO, SP
Plecoptera	Perlodidae	*Aphroperlodes*	=	=	=	=	=	=	=	=	=	=	=	Coded as mean of Perlodidae	AL, MO
	Perlodidae	*Hemimelaena*	X	X	X	X	X	X	X	X	X	X	X		PO
	Leuctridae	*Tyrrhenoleuctra*	X	X	X	X	X	X	X	X	X	X	X		AL, PO, SP
Heteroptera	Corixidae	*Heliocorisa*	=	=	=	=	=	=	=	=	=	X	=	Coded as mean of Corixidae	SP
	Gerridae	*Aquarius*	X	X	X	X	X	X	X	X	X	X	X		MO, SP
	Hebridae	*Hebrus*	0	0	0	X	X	X	X	X	X	0	0		AL, FR, IT, LE, MO, SP
	Veliidae	*Rhagovelia*	=	X	=	X	=	=	=	X	X	X	X	Coded as mean of Veliidae	LE, SP
Odonata	Aeschnidae	*Caliaeschna*	=	=	=	=	=	=	=	=	=	=	=	Coded as mean of Aeshnidae	LE
	Coenagrionidae	*Cercion*	=	X	X	=	=	=	=	=	=	=	=	Coded as mean of Coenagrionidae	SP
	Euphaeidae	*Epallage*	=	=	=	=	=	=	=	=	=	=	=	Coded as mean of Calopterygidae	IS, LE
	Gomphidae	*Lindenia*	=	=	=	=	=	=	=	=	=	=	=	Coded as mean of Gomphidae	FR

Cont.

Table 2. *cont.*

Group	Family	Genus	Maximal size	Life cycle duration	Potential number of reproduction cycles per year	Aquatic stages	Reproduction	Dissemination	Resistance forms	Respiration	Locomotion and substrate relation	Food	Feeding habits	Comments	Country
	Libellulidae	*Diplacodes*	X	X	X	X	X	X	=	X	X	X	=	Coded as mean of Libellulidae	SP
	Libellulidae	*Trithemis*	=	=	=	=	=	=	=	=	=	=	=	Coded as mean of Libellulidae	IT
Coleoptera	Dytiscidae	*Canthydrus*	=	=	=	X	=	X	=	X	X	X	X	Coded as mean of Dytiscidae	SP
	Dytiscidae	*Herophydrus*	X	=	=	X	=	X	=	X	X	X	X	Coded as mean of Dytiscidae	SP
	Elmidae	*Grouvellinus*	=	X	=	=	=	=	=	=	=	=	=	Coded as mean of Elmidae	IS, LE
	Hydrophilidae	*Coelostoma*	=	=	=	X	=	=	=	=	X	=	X	Coded as mean of Hydrophilidae	MO, SP
	Hydrophilidae	*Cymbiodyta*	=	=	=	=	=	=	=	=	=	=	=	Coded as mean of Hydrophilidae	AL
	Ochtheridae	*Ochterus*	X	0	0	0	0	0	0	0	0	0	0		SP
Diptera	Athericidae	*Ibisia*	=	=	X	=	=	=	=	=	=	=	=	Coded as *Atherix*	AL, FR, IT, LE
	Blephariceridae	*Apistomyia*	=	=	=	=	=	=	=	=	=	=	=	Coded as mean of Blephariceridae	FR
	Blephariceridae	*Dioptopsis*	=	=	=	=	=	=	=	=	=	=	=	Coded as mean of Blephariceridae	FR
	Scatophagidae	*Acanthocnema*	=	=	=	=	=	=	=	=	=	X	X	Coded using information on Anthomyidae	SP

and NEW. In turn, MED and NEW overlapped along the first between-class FCA axis but were clearly separated along the second between-class FCA axis, which explained 36 % of the trait variability (Fig. 1). We also performed between-class FCA using pairs of tables. Differences between MED and TEM accounted for 3.1 % of the explained variability (simulated $P = 0.001$), whereas differences between MED and NEW and TEM and NEW accounted for 2.0 % and 3.2 %, respectively, of the explained variability (simulated $P = 0.001$), confirming the separation observed on the first two axes of the above global FCA.

From the 31 *a priori* hypotheses on trait categories for MED, TEM and NEW (Table 1), 27 included enough genera to be tested for significance (i.e., more than 10 genera). When MED and TEM were compared, 8 trait categories significantly agreed with our hypotheses, 3 significantly contradicted our hypotheses, and 16 did not show significant differences (Table 4). MED and TEM genera mostly differed on the following traits: dissemination, locomotion and sub-

strate relation. A comparison of NEW vs. MED genera showed that 13 categories did not have significant differences, 8 categories agreed with our hypothesis (i.e., NEW genera had significantly more mediterranean characteristics than MED genera), and 6 contradicted our hypothesis (Table 4). Thus, NEW genera significantly comprised more genera with larger maximal sizes, shorter life cycles, imago stages, ovoviviparity and diapause and ability to feed on living microphytes as scrapers. However, NEW genera were not necessarily swimmers nor did they have higher aerial active dissemination and spiracles. Comparisons between NEW and TEM genera showed that 21 categories did not show significant differences, 5 categories showed differences in agreement with our hypotheses (i.e., NEW genera had significantly more mediterranean characteristics than TEM genera), and only 1 contradicted our hypothesis. Thus, compared with TEM genera, NEW genera had smaller or larger sizes and a dominance of diapausing organisms, fliers and scrapers.

Table 3. Biological traits (letter a-i) and their categories (number) for each genera not included in Tachet *et al.* (2002) but present in mediterranean rivers surveys (see Table 1 for codes of categories). *Rasgos biológicos (letras a-i) y categorías (número) para cada género no incluido en Tachet* et al. *(2002) pero presentes en muestreos de ríos mediterráneos (ver Tabla 1 para los códigos de las categorías).*

Genus	a1a2a3a4a5a6a7b1b2c1c2c3d1d2d3d4e1e2e3e4e5e6e7e8f1f2f3f4g1g2g3g4g5j1j2j3j4u1u2u3u4u5u6u7u8h1h2h3h4h5h6h7h8h9i2i3i4i5i6i7i8
Limnatis	0 0 0 0 0 3 1 0 3 3 0 0 1 3 0 2 0 0 0 3 0 0 2 0 3 1 1 0 0 3 0 0 0 3 0 0 0 0 0 0 3 0 0 2 0 0 0 0 0 0 0 0 0 0 3 0 0 0 0 2 0 2
Belgrandiella	0 2 1 0 1 0 0 2 1 0 2 1 2 1 0 3 1 0 2 0 0 0 0 3 1 1 0 0 0 0 2 1 2 2 0 0 0 0 0 3 1 0 0 0 0 1 3 2 2 1 0 0 0 0 2 3 0 0 0 0
Mercuria	0 3 3 0 0 0 0 1 3 0 0 0 0 3 0 3 2 0 2 0 0 0 0 0 2 1 0 0 0 0 0 3 0 3 0 0 0 0 0 0 3 0 0 0 0 0 3 1 1 0 0 0 0 0 0 2 3 0 0 0 0
Pseudamnicola	0 0 0 1 3 1 0 2 1 0 1 1 0 3 0 3 2 0 2 0 0 0 0 0 2 1 2 2 0 0 0 0 0 3 1 0 0 0 0 1 3 2 2 1 0 0 0 0 2 3 0 0 0 0
Sadleriana	0 2 1 0 1 0 0 2 1 0 1 1 2 2 0 3 2 0 2 0 0 0 0 3 1 1 0 0 0 0 2 1 2 2 0 0 0 0 0 3 1 0 0 0 0 1 3 2 2 1 0 0 0 0 2 3 0 0 0 0
Semisalsa	0 2 1 0 1 0 0 2 1 0 2 1 2 1 0 3 1 0 2 0 0 0 0 3 1 1 0 0 0 0 2 1 2 2 0 0 0 0 0 3 1 0 0 0 0 1 3 2 2 1 0 0 0 0 2 3 0 0 0 0
Syrofontana	0 2 1 0 1 0 0 2 1 0 2 1 2 1 0 3 1 0 2 0 0 0 0 3 1 1 0 0 0 0 2 1 2 2 0 0 0 0 0 3 1 0 0 0 0 1 3 2 2 1 0 0 0 0 2 3 0 0 0 0
Fagotia	0 0 1 3 2 0 0 3 0 0 1 3 0 3 0 3 2 0 0 3 0 0 0 1 2 1 0 0 0 0 0 3 0 3 0 0 0 0 0 0 3 0 0 0 0 0 1 3 2 0 0 0 0 0 0 3 0 0 0 0 0
Melanopsis	0 0 1 3 2 0 0 3 0 0 1 3 0 3 0 3 2 0 0 3 0 0 0 1 2 1 0 0 0 0 0 3 0 3 0 0 0 0 0 0 3 0 0 0 0 0 1 3 2 0 0 0 0 0 0 3 0 0 0 0 0
Amphimelania	0 0 2 3 0 0 0 0 0 0 0 0 3 0 0 3 3 0 0 0 0 0 0 3 1 0 0 0 0 0 3 0 3 0 0 0 0 0 0 3 0 0 0 0 1 3 1 3 0 0 0 0 0 3 1 3 0 0 0 0
Melanoides	0 0 0 0 3 1 0 0 0 0 0 0 3 0 0 3 3 0 0 0 0 0 0 3 3 1 0 0 0 0 0 3 0 3 0 0 0 0 0 0 3 0 0 0 0 1 3 1 3 0 0 0 0 0 3 1 3 0 0 0 0
Bulinus	0 0 1 3 0 0 0 1 3 3 3 1 3 0 0 3 0 0 0 3 0 0 0 0 2 1 0 0 0 0 0 1 1 3 0 0 0 0 1 0 3 0 0 0 0 0 0 3 2 2 0 1 0 0 0 0 1 3 0 0 0 0
Succinea	0 0 0 3 1 0 0 3 2 1 3 0 3 0 0 2 0 0 0 3 1 0 0 0 2 2 0 0 0 0 0 2 0 3 0 0 0 0 1 0 3 0 0 0 0 0 1 2 3 0 3 0 2 0 0 1 3 0 0 2 0
Metacrangonyx	0 0 0 1 3 0 0 1 3 0 0 3 3 3 0 3 3 0 0 0 0 0 0 0 3 2 0 0 0 0 0 0 3 0 3 0 0 2 3 0 1 0 0 0 1 5 2 1 2 2 1 0 0 3 1 0 0 0 0
Palaemon	0 0 0 0 3 1 0 3 1 0 2 3 3 3 0 3 3 0 0 0 0 0 0 0 3 3 0 0 0 0 0 3 0 3 0 0 0 0 3 0 0 0 0 0 0 2 2 0 3 2 3 0 2 3 1 0 0 0 0
Palaemonetes	0 0 0 0 3 1 0 3 1 0 2 3 3 3 0 3 3 0 0 0 0 0 0 0 3 3 0 0 0 0 0 3 0 3 0 0 0 0 3 0 0 0 0 0 0 2 2 0 3 2 3 0 2 3 1 0 0 0 0
Centroptiloides	0 0 3 0 0 0 0 3 0 0 1 3 3 3 0 0 1 0 2 1 0 0 0 0 2 2 1 2 1 0 0 0 2 1 2 0 0 0 3 2 0 0 0 0 2 1 3 1 0 0 0 0 2 3 0 0 0 0
Nigrobaetis	0 0 3 0 0 0 0 3 0 0 1 3 3 3 0 0 1 0 2 1 0 0 0 0 2 2 1 2 1 0 0 0 2 1 2 0 0 0 3 2 0 0 0 0 2 1 3 1 0 0 0 0 2 3 0 0 0 0
Afronurus	0 0 0 3 0 0 0 3 1 1 3 0 3 3 0 0 0 2 0 3 0 0 0 0 3 1 1 3 2 0 0 1 2 1 3 0 0 0 0 1 5 0 0 0 0 0 1 2 3 2 0 0 0 0 0 2 3 0 0 0 0
Isonychia	0 0 3 0 0 0 0 3 0 0 3 0 3 3 0 0 0 3 1 0 0 0 0 0 3 1 1 2 3 0 0 0 0 1 3 0 0 0 0 1 4 0 0 0 0 1 2 0 3 0 0 0 0 0 0 2 0 2 3 0 0 0
Oligoneuriopsis	0 0 0 3 0 0 0 3 0 0 3 0 3 3 0 0 0 3 1 0 0 0 0 0 3 1 1 2 3 0 0 0 0 1 3 0 0 0 0 0 3 0 0 0 0 1 2 0 3 0 0 0 0 0 0 2 0 2 3 0 0 0
Tyrrhenoleuctra	0 3 1 0 0 0 0 3 0 0 3 0 3 3 0 0 0 0 0 0 0 3 0 0 0 2 2 0 1 0 0 0 3 0 3 0 0 0 0 0 3 0 0 0 0 0 2 3 0 0 0 0 0 0 1 3 0 0 0 0 0
Aphroperlodes	0 0 2 1 0 0 0 2 1 0 2 1 2 3 2 1 1 1 1 1 1 0 0 1 0 1 1 1 1 0 0 0 1 1 1 1 0 1 0 1 1 2 1 0 0 0 0 1 1 2 1 0 1 1 0 1 0 1 0 1 0 1 1 0
Hemimelaena	0 0 0 3 0 0 0 3 0 0 3 0 3 3 0 0 0 0 0 3 0 0 0 2 2 0 1 2 0 0 0 1 3 0 0 0 0 0 3 0 0 0 0 0 1 1 2 0 0 0 4 0 0 3 0 0 0 1 0
Caliaeschna	0 0 0 0 2 2 0 1 3 3 1 0 2 3 0 0 0 0 0 0 0 3 1 0 1 1 0 3 1 0 0 1 2 1 3 0 0 0 0 0 5 0 0 0 0 0 0 0 0 0 0 1 4 1 0 0 0 0 0 3 0
Cercion	0 0 0 3 1 0 0 3 0 0 1 3 2 3 0 0 0 0 0 3 0 0 1 1 0 3 0 0 0 1 3 1 3 0 0 0 0 1 5 0 0 0 0 0 0 0 0 0 1 4 0 0 0 0 0 3 0
Epallage	0 0 0 1 3 1 0 2 2 1 3 0 3 3 0 0 0 0 0 0 3 0 0 2 1 0 2 0 0 0 2 2 1 3 0 0 0 1 4 0 0 0 0 0 0 0 0 0 0 5 0 0 0 0 0 3 0
Lindenia	0 0 0 0 3 0 0 0 3 2 1 0 3 3 0 0 0 2 2 0 0 0 0 0 2 1 0 3 2 0 0 0 1 1 3 0 0 0 0 2 4 0 0 0 0 0 0 0 0 0 0 5 0 0 0 0 0 3 0
Diplacodes	0 0 0 2 1 0 0 1 1 1 1 1 3 3 0 0 0 2 1 0 0 0 0 0 1 1 0 3 1 0 0 1 2 1 3 0 0 0 0 1 3 0 0 0 0 0 0 0 0 0 3 0 0 0 0 0 3 0
Trithemis	0 0 0 2 2 0 0 1 2 2 1 1 3 3 0 0 0 2 2 0 0 0 0 0 0 1 1 0 3 1 0 0 1 2 1 3 0 0 0 0 1 4 1 0 0 0 0 0 0 0 0 0 5 0 0 0 0 0 3 0
Heliocorisa	0 0 2 0 0 0 0 3 0 0 1 2 3 3 0 2 0 0 1 3 0 0 0 0 1 2 0 2 0 0 0 1 0 1 0 2 3 1 0 5 0 0 0 0 0 3 3 3 0 0 0 0 0 0 2 1 0 3 0 0
Aquarius	0 0 0 3 0 0 0 3 2 0 1 3 1 2 0 2 0 0 3 0 0 1 0 1 2 3 0 0 0 3 0 0 0 0 3 3 4 0 0 0 0 0 0 0 0 0 0 0 0 0 3 0 0 0 0 0 3 0
Hebrus	0 0 0 0 0 0 0 0 0 0 3 3 0 3 0 0 0 3 0 0 1 0 1 2 1 3 0 0 0 3 0 0 0 0 3 1 2 0 3 0 0 0 0 0 0 0 0 3 0 3 0 0 0 0 0 3 0 0
Rhagovelia	3 0 0 0 0 0 0 3 0 0 2 3 0 3 0 3 0 0 0 3 0 0 2 0 1 2 1 1 0 0 0 3 0 0 0 0 3 1 3 0 0 0 0 0 0 0 0 0 0 1 3 1 0 0 0 0 0 3 1 0
Canthydrus	0 2 1 1 0 0 0 1 3 0 2 2 3 3 0 3 0 0 0 3 0 0 0 1 1 0 3 0 0 0 0 3 1 0 0 3 1 0 3 3 0 0 0 0 0 0 0 0 0 0 0 2 3 0 0 3 0 0 3 0 0
Herophydrus	0 3 0 0 0 0 0 1 3 0 2 2 3 3 0 3 0 0 0 3 0 0 0 0 1 1 0 3 0 0 0 0 3 1 0 0 3 1 0 3 3 0 0 0 0 0 0 0 0 0 0 0 2 3 0 0 3 0 0 3 0 0
Grouvellinus	0 3 0 0 0 0 0 3 0 3 0 3 3 0 2 0 0 0 3 0 0 0 0 2 1 0 2 0 0 0 0 3 1 3 3 0 1 0 0 4 0 1 0 0 0 1 0 3 0 0 0 0 0 1 3 0 0 0 0
Coelostoma	0 2 1 0 0 0 0 1 3 0 3 1 3 3 0 3 0 0 0 2 0 0 0 0 0 1 0 3 0 0 0 0 3 1 0 1 3 1 0 3 3 0 0 0 0 0 0 0 0 0 3 0 0 3 1 0 3 2 0 0 0 1 0
Cymbiodyta	0 2 1 0 0 0 0 1 3 0 3 1 3 3 0 2 0 0 0 2 0 0 0 0 0 1 0 3 0 0 0 0 3 1 0 1 3 1 0 3 3 0 0 0 0 0 0 0 0 0 3 0 0 3 1 0 0 3 0 0 0 1 0
Ochterus	0 3 3 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 3 0 0 0 0 0 3 0 0
Ibisia	0 0 0 0 3 0 0 3 1 0 3 0 0 3 0 0 0 0 0 0 0 0 3 0 0 1 0 1 0 0 0 0 3 0 1 0 0 0 0 3 0 1 0 0 0 0 0 0 0 0 0 0 3 0 0 0 0 0 3 0 0
Apistomyia	0 0 3 0 0 0 0 3 0 0 3 1 2 3 2 0 0 0 0 3 0 0 0 2 1 0 1 1 0 0 3 0 1 3 0 0 0 0 0 2 0 0 2 1 0 0 0 5 0 0 0 0 0 0 0 3 0 0 0 0
Dioptopsis	0 0 3 0 0 0 0 3 0 0 3 1 2 3 2 0 0 0 0 3 0 0 0 2 1 0 1 1 0 0 3 0 1 3 0 0 0 0 0 2 0 0 2 1 0 0 0 5 0 0 0 0 0 0 0 3 0 0 0 0
Acanthocnema	0 0 3 1 0 0 0 3 0 0 1 3 0 2 1 0 1 0 1 1 0 0 3 0 0 1 0 0 0 0 0 0 3 0 0 0 3 0 0 0 4 1 0 0 0 0 1 0 0 0 0 0 3 0 1 0 0 0 0 3 0

DISCUSSION

We used available literature and consulted several taxonomic specialists to code traits for 44 genera found in the Mediterranean Basin but that were not included in Tachet's database. These NEW genera belonged to different taxonomic groups; Mollusca encompassed the highest number of non-coded genera. Although Mollusca has more species in the Paleartic than in other zoogeographical regions (Strong *et al.*, 2008), some families are recognized to have a Gondwana origin (Ponder & Walker, 2003; Strong *et al.*, 2008) and therefore could have been present in North
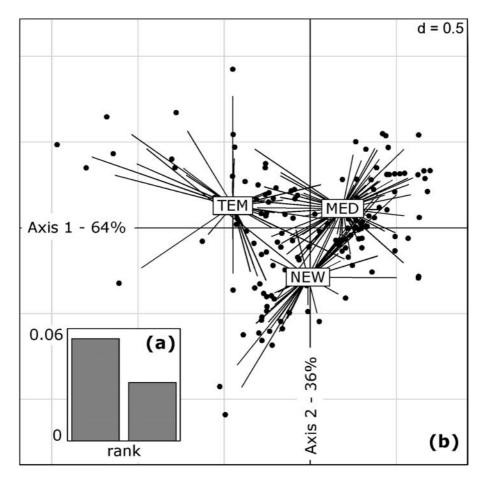
Figure 1. Result of a between-class fuzzy correspondence analysis (FCA) performed on the 11 traits-by-genera array showing (a) the histogram of eigenvalues and (b) the first two axes factorial map. Genera (dots) are linked to a given group by a line. MED for mediterranean genera, TEM for temperate genera and NEW for new-coded mediterranean genera. *Resultado del análisis de correspondencias difusas entre tipos de géneros (FCA) realizado con los datos de 11 rasgos biológicos y mostrando (a) el histograma de valores propios y (b) el mapa factorial de los dos primeros ejes. Los géneros (puntos) están unidos a su correspondiente grupo con una línea. MED indica géneros mediterráneos ya codificados, TEM indica géneros de la región templada, y NEW nuevos géneros mediterráneos no codificados.*

Africa for a long time. This is the case of Hydrobiidae, the family from which we found the most genera not included in the Tachet's database, and Thiaridae, for which we also found a non-coded genus in Morocco. In addition, some of these genera, such as *Bulinus,* are widely documented in African and Asian regions (e.g., Chu *et al.*, 1968; Kluste & Baleux, 1996; Laamrani & Boelee, 2002), and their distribution is constrained to the Mediterranean Basin. However, 4 Mediterranean Basin regions appear as a hotspot for Molluscan biodiversity, and overall lower diversity has been found at higher latitudes

(Strong *et al.*, 2008). Other taxonomic group characteristics from mediterranean rivers (Heteroptera, Odonata and Coleoptera, Bonada *et al.*, 2007a) also contained genera not coded in Tachet's database. Interestingly, Ribera (2000) showed that the Iberian Peninsula was very rich in Coleoptera, and it is considered a hotspot of Dytiscidae. Although we used more sites from Spain than from other countries, of the 6 non-coded Coleoptera that we found, only 4 were solely present in Spain, and 2 of those were Dytiscidae.

In a previous study, we found that macroinvertebrate composition in mediterranean and tem-

perate rivers differed in trait composition, and those differences concerned traits that were associated with higher resilience and resistance to seasonal flow variability in the Mediterranean Basin (Bonada *et al.*, 2007a). Therefore, it is not surprising that we found similar results when analysing the trait profile of exclusive genera found in each climatic region. When significant, our trait predictions between MED and TEM genera were confirmed. According to our

Table 4. Mean affinity values expressed as the per cent of all mediterranean (MED), temperate (TEM) and new coded mediterranean (NEW) genera for each biological trait category, showing results of the Kruskal-Wallis non-parametric tests between pairs of genera types. Only traits for which we could provide *a priori* predictions for the mediterranean region are presented (Table 1). The term "no data" indicates that there were less than 10 genera with information for that category; therefore, the mean values and tests are not presented. The Kruskal-Wallis non-parametric test was not performed for those categories lacking enough genera (e.g., a1, a6, e8, g3, u2, u6, h5) and, therefore, is not presented. For all tests, (0) indicates that no significant differences were found. For MED vs. TEM test, (+) indicates that results follow our predictions and (-) indicates the opposite pattern. For MED vs. NEW and TEM vs. NEW tests, (++) indicates that, according to our predictions, a NEW genera has significant mediterranean characteristics for that category, whereas (–) indicates the opposite pattern. *Valores de afinidad medios (en %) de los géneros mediterráneos (MED) y templados (TEM) codificados y los no codificados (NEW) para cada categoría de rasgos biológicos, junto con resultados de los análisis no paramétricos Kruskal-Wallis entre tipos de géneros. Sólo se presentan las categorías para las que se puedieron establecer predicciones a priori para el Mediterráneo (Table 1). "No data" indica que había menos de 10 géneros con información para esa categoría y, por lo tanto, no se presentan las medias. Asimismo, para aquellas categorías con insuficiente número de genéros, no se calculó el test no paramétrico Kruskal-Wallis y, por lo tanto, no se presentan (i.e. a1, a6, e8, g3, u2, u6, h5). Para todos los análisis, un (0) indica que no hubo diferencias significativas. Para el análisis entre MED y TEM, un (+) indica que los resultados siguen nuestras predicciones y un (–) el contrario. Para los análisis entre MED vs. NEW y TEM vs. NEW, un (++) indica que, según nuestras predicciones, un género NEW tiene características significativamente más mediterráneas para esa categoría, mientras que un (–) indica el contrario.*

Trait	Category	Code	Mean (%)			Kruskal-Wallis Tests		
			TEM	MED	NEW	TEM vs. MED	TEM vs. NEW	MED vs. NEW
Maximal size	> 0.25 – 0.5 cm	a2	4	24	18	(+)	(++)	0
	> 0.5 – 1 cm	a3	26	23	no data	0		
	> 1 – 2 cm	a4	42	24	24	(+)	0	0
	> 2 – 4 cm	a5	11	20	23	0	0	0
Life cycle duration	≤ 1 year	b1	59	47	63	0	0	(++)
Potential number of reproduction cycles per year	< 1	c1	19	14	no data	0		
Aquatic stages	larva	d2	37	42	40	(–)	0	0
	imago	d4	14	15	24	0	(++)	(++)
Reproduction	Ovoviviparity	e1	19	no data	no data			
	Clutches, terrestrial	e7	no data	7	no data			
Dissemination	Aquatic passive	f1	31	16	38	(+)	0	(++)
	Aerial active	f4	28	48	26	(+)	0	(–)
Resistance forms	Diapause or dormancy	g4	20	20	43	0	(++)	(++)
	None	g5	44	66	42	(–)	0	(–)
Respiration	Gill	j2	25	27	39	0	0	0
	Plastron	j3	no data	4	no data			
	Spiracle (aerial)	j4	9	31	18	(+)	0	(–)
Locomotion and substrate relation	Flier	u1	1	6	4	(+)	(++)	0
	Swimmer	u3	8	25	16	(+)	(++)	(–)
	Crawler	u4	67	52	60	(+)	0	0
Food	Plant detritus ≥ 1 mm	h3	19	7	no data	0		
	Living microphytes	h4	12	13	no data	0		
Feeding habits	Shredder	i3	31	36	26	0	0	0
	Scraper	i4	11	10	no data	0		

predictions in Table 1, some trait categories of NEW genera were even more mediterranean-like that those of MED, whereas the trait categories of other NEW genera were not. Different trait combinations allow organisms to cope with specific environmental conditions. For mediterranean river ecosystems, predictable floods and droughts are major constraints for freshwater macroinvertebrates (Gasith & Resh, 1999), and organisms can cope with them in different ways. For example, MED genera use aerial active dissemination that allows organisms to escape from a drought; NEW genera have diapause, which is also a strategy to avoid survive droughts (Williams, 2006). Interestingly, we were able to show that almost all trait categories that significantly differed between NEW and TEM genera indicated that NEW genera had more mediterranean characteristics, which agreed with our main hypothesis. Therefore, our results suggest that some biological traits for NEW genera allow them to successfully inhabit mediterranean rivers. This finding may explain why these genera have not been extensively found in temperate Europe and why they were not included in Tachet's database. However, we cannot discount other explanations. Although fliers were more frequent in NEW than in TEM genera, NEW genera had no strong aerial active dissemination, that is, the trait category f4 was significantly less frequent in NEW genera than in MED genera; therefore, NEW genera have a limited overland dissemination that may hamper their success in temperate Europe (Bohonak & Jenkins, 2003). Additionally, the 44 NEW genera seem to be rare in the Mediterranean Basin. Seventeen genera out of these 44 genera were only found in a single site of the 488 sites in the Mediterranean Basin (a per cent of occurrence equal to 0.2), whereas the genera that occurred most frequently were the Prosobranchia *Melanopsis* and *Mercuria* (a per cent of occurrence equal to 9.0 and 5.3, respectively). Finally, we acknowledge that not all of these genera have been exclusively found in this region, and most of them have been also recorded in temperate Europe (see Fauna Europaea Web Service, 2004). However, we did not find them in the TEM genera database, which in-

cluded 344 sites scattered across Europe and covered different river types (Statzner *et al.*, 2007). This finding may indicate that their occurrence outside of the Mediterranean Basin is also very low. Therefore, we conclude that mediterranean genera not included in Tachet's database are rare genera with low dispersal abilities but that they have some mediterranean trait characteristics that allow them to cope with drought periods. As the knowledge of the fauna in the Mediterranean Basin increases, we can expect new genera to be added to the list. Similarly, as new biological information from these new genera or from existing genera is generated, Tachet's database should be revisited, and the fuzzy coding should be modified accordingly. We encourage our Mediterranean Basin colleagues to provide information on the biological traits of all of these genera to improve our knowledge on macroinvertebrate communities and their functional characteristics.

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