Taxonomic and biological trait differences of stream macroinvertebrate communities between mediterranean and temperate regions: implications for future climatic scenarios

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Abstract

Streams in mediterranean regions have highly seasonal discharge patterns, with predictable torrential floods and severe droughts. In contrast, discharge is less variable in temperate regions and intermittent flow conditions are uncommon. Hydroclimatic models predict that climate change would increase frequency and severity of floods and droughts across Europe, thus increasing the proportion of streams with mediterranean characteristics in actually temperate areas. Correspondingly, understanding actual ecological differences between mediterranean and temperate streams may help to anticipate large-scale ecological impacts of climate change. Given that large-scale factors determine local community composition, we hypothesized that climatic differences between mediterranean and temperate regions should affect the taxonomic and biological trait composition in streams. We assembled the abundance of stream macroinvertebrate genera of 265 sites each from the Mediterranean Basin and from temperate Europe and linked these abundances to published information on 61 categories of 11 biological traits reflecting the potential of resilience from and resistance to disturbances. Although regional taxonomic richness was higher in the mediterranean than in the temperate region, local taxonomic richness and diversity did not significantly differ between regions. Local trait richness and diversity were significantly higher in the mediterranean region. Both local taxonomic and trait-community composition differed between regions, but the former varied much more than the latter, highlighting that climate change could produce large changes in the taxonomic but rather weak changes in the trait composition. The mediterranean region was characterized by macroinvertebrates with higher dispersion and colonization capabilities, suggesting that species loss in the temperate region, by extinction or northward emigration of taxa, would be compensated for by immigration of southern mediterranean taxa. Thus, climate change would likely have stronger implications for the local conservation of taxa than for the trait composition of stream macroinvertebrate communities.

Keywords: climate change, Europe, function, Mediterranean Basin, regional and local diversity, structure, temporary streams

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Introduction

Assessments of global patterns of climate change forecast a general increase of temperature and total pre-

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cipitation, but with important regional differences, especially in precipitation (Arnell, 1999a; Johns *et al.*, 2003). For Europe and different future climate scenarios, models predict regional temperature increases and more variable precipitation patterns (www.grida.no/ climate/ipcc_tar/wg2/495.htm). Annual precipitation is predicted to increase in northern Europe, decrease in southern Europe, and remain stable in central Europe. In addition, seasonal precipitation patterns across Europe would change: winter–spring precipitation

would increase and summer–autumn precipitation would decrease (Déqué et al., 1998; Johns et al., 2003; Giorgi et al., 2004). Precipitation affects the discharge of running waters (Swift et al., 1988) (i.e. their hydrological patterns would be modified by changes in precipitation and temperature effects on evapotranspiration; Lindh, 1992; Arnell, 1999a,b). Hydroclimatic models predict that European rivers would collectively show reduced discharge (Arnell, 1999a,b) and seasonally would have higher winter and lower summer flow, mainly because snow storage would be reduced (Arnell, 1999a,b; Middelkoop et al., 2001; Eckhardt & Ulbrich, 2003; Graham, 2004). Although all these patterns could regionally and subregionally vary, it seems that floods and droughts would become more severe and frequent across Europe (see e.g. www.cru.uea.ac.uk/cru/projects/mice/) (i.e. seasonal discharge patterns in temperate areas, particularly in central Europe, would acquire mediterranean characteristics; e.g. Arnell, 1999a,b). Thus, assessing actual ecological differences of streams between the mediterranean region of the Mediterranean Basin and temperate Europe is an approach that may anticipate large-scale ecological impacts of climate change (Álvarez-Cobelas et al., 2005). This paper, therefore, compares stream macroinvertebrate communities in mediterranean and temperate regions in terms of taxonomy (i.e. structure) and biological traits (i.e. function, given that the traits directly or indirectly indicate ecological functions; Statzner et al., 2004; Bonada et al., 2006b).

Abundant empirical evidence suggests that recent climate changes induced varying structural (e.g. species loss, changes in species' distribution) and functional (e.g. phenology, migration, body size) ecological responses among organisms (Walther et al., 2002; Parmesan, 2006). Most of these studies, however, focused at local scales and single species (Parmesan, 2006). Extrapolation from low (single species) to high (community or ecosystems) levels of organization is difficult and climate change is typically viewed as a large-scale phenomenon (Walther et al., 2002). Therefore, studies at larger spatial scales and higher biological organizational levels are thus required to anticipate impacts of climate change. In this context, few studies so far focus on the structural (Pounds et al., 1999; Sagarin et al., 1999) or the functional community level (Mulholland et al., 1997; Lake et al., 2000; Moline et al., 2004).

Explaining the presence and abundance of species in communities at various spatial scales is a continuing goal in ecological research. Several geological and environmental factors, including climatic characteristics (e.g. Dingle et al., 2000; Forsman & Mönkkönen, 2003; Lindsay & Bayoh, 2004), often act hierarchically at different scales to select only those organisms that have

matching biological traits (Poff & Ward, 1990; Poff, 1997; Statzner et al., 2001b). Differences in morphological, behavioural, and physiological traits of individual species are, thus, common along climatic gradients (Chapin & Chapin, 1981; Murray et al., 2004; Thuiller et al., 2004) (i.e. regions with similar climatic characteristics should support organisms with similar biological traits, whereas regions differing in climate should have organisms with different traits). Consequently, trait and species composition should alter with changing climate (Díaz & Cabido, 1997; Mulholland et al., 1997).

Hot and dry summers and cool and wet winters characterize mediterranean climate (Aschmann, 1973), whereas summers are milder and winters colder and wetter in temperate regions. These differences between both regions, in addition to other large-scale factors (e.g. geological processes, such as glaciations), affect the structure and function of terrestrial communities. The stress of mediterranean summer droughts, for example, plays an important evolutionary role evolving terrestrial organisms with resilience or resistance strategies such as low metabolic rates, short life spans with an early maturity, less permeable cuticles, higher water contents in summer, cryptobiosis, and parthenogenesis (Stamou, 1998). By contrast, the structural and functional adaptation differences between the aquatic macroinvertebrate communities of the mediterranean regions (highly variable seasonal discharge, predictable torrential floods, and severe droughts) and temperate regions (less variable, typically permanent discharge) (Gasith & Resh, 1999) are largely unknown.

We, thus, tested six hypotheses: (1) given that the Mediterranean Basin has been considered a biodiversity hotspot for several reasons (Myers et al., 2000), regional taxa richness should be higher there than in the temperate region (Ricklefs, 1987), (2) consequently, local taxa richness in the mediterranean region should perhaps be higher than in the temperate region (Ricklefs, 1987), (3) large-scale climatic differences should cause regional differences in the taxonomic community composition (Poff & Ward, 1990), (4) likewise, large-scale climatic differences should cause differences in the trait-community composition (Poff & Ward, 1990), (5) compared with the taxonomic structure, stream macroinvertebrate traits are less affected by biogeographical constraints and vary relatively little across large spatial and temporal scales (Statzner et al., 2001a, 2004, 2005; Hausner et al., 2003), hence we hypothesized that the taxonomic differences of communities between mediterranean and temperate regions would be greater than the trait differences, and (6) differences in seasonal discharge patterns, habitat availability, and other stream ecosystem

characteristics between mediterranean and temperate regions should affect several (not all) biological traits (see Table 1); thus, if predictions would be confirmed and stream macroinvertebrates in mediterranean regions would have indeed higher dispersion (e.g. aerial active) and colonization (e.g. asexual reproduction or ovoviviparity, enabling the foundation of new populations) abilities, climatic-change-induced regional loss of temperate species through extinction or northward displacements would be compensated for by immigration of mediterranean taxa and potentially changing community structure and function in actually temperate regions.

Materials and methods

We tested our six hypotheses using large databases on macroinvertebrate communities in streams in mediterranean (M) and temperate (T) regions of the Mediterranean Basin and Europe. Database origin and structure were described in Statzner *et al.* (in press). Here, we communicate only essentials required to understand this paper.

Site selection

Statzner *et al.* (in press) assembled stream macroinvertebrate abundance data for 527 natural or almost-natural (least human-impacted) sites of mediterranean and temperate Europe that were complemented with new records from South Europe, Middle East, and North Africa (Khalaf & Lahoud, 1983; Khalaf, 1984; Ajakane, 1988; Badri, 1993; Gumiero, 1993; Ouahsine, 1993; Zouakh, 1995; Girgin & Kazanci, 1997; Berrahou *et al.*, 2001; Maamri *et al.*, 2005; N. Skoulikidis & K. Gritzalis, personal communication, 2005).

Of a total of 609 sites for which data were available, 265 were located in M and 344 in T, with 145 T-sites on the British mainland. To balance site numbers between regions, 66 British sites were randomly selected, and the resulting T database (265 sites) was used for subsequent analyses. The 530 sites were distributed from Scandinavia to Morocco and Turkey. The distinction between M and T was at the macroclimate scale (Oliver & Hidore, 2002) and ignored mesoscale differences (e.g. high-mountain sites in the Sierra Nevada of southern Spain were included in M). Köppen climatic maps (1931) based on physical features (Fig. 1) served to classify sites into M or T. The term 'temperate' covers several European biogeographical provinces from continental to oceanic macroclimates.

Macroinvertebrate abundance

Statzner *et al.* (in press) assessed mean annual site abundances of macroinvertebrate genera (at 344 T- and 183 M-sites) and showed that the natural variability in the taxonomic abundance structure of the macroinvertebrate communities was greater than that caused by the use of different methods. By comparison with T, seasonal variability in macroinvertebrate richness and abundance could be greater in M (now including sites from the Middle East and North Africa) because of high variability in discharge regimes and temporary conditions in many reaches. We thus analysed for 81 M-sites at all four seasons, using log-transformed macroinvertebrate abundances, Euclidean distances among sites for each season and the annual mean. Mantel tests were used to check for significance using random permutations. Seasonal abundances were highly correlated with the annual mean abundance of the populations (for all four seasons, correlations ≥ 0.73, $P < 0.001$), suggesting that each season was representative for M-sites.

Environmental characteristics

To understand differences between M and T, and explore within-region variability, environmental site data coded by categories were used (see Statzner *et al.*, in press). The following data were included: altitude (lowlands, highlands, and mountains for <150, $150–1000$, and >1000 m a.s.l., respectively), water hardness (soft, intermediate, and hard for approximately <200, $200–400$, and $>400\,\mu S\,cm^{-1}$, respectively), stream width (small, intermediate, and large for <10, $10–40$, and >40 m, respectively), and flow permanency (permanent or temporary). More precise quantification of environmental variables was not possible but these factors are generally considered as major determinants for stream macroinvertebrate community composition (e.g. Bonada *et al.*, 2005).

Biological traits

Macroinvertebrate communities were also characterized using 11 biological traits and 61 categories (Usseglio-Polatera *et al.*, 2000; Tachet *et al.*, 2002). These traits describe life-cycle features (life-cycle duration, reproductive cycles per year, aquatic stages), resilience or resistance potentials (dispersal, locomotion, resistance forms), physiology and morphology (respiration, maximum size), and reproduction and feeding behaviour (reproduction, food, and feeding habits). Within the database, each genus was coded according to its affinity to each category of a trait using a fuzzy coding approach (Chevenet *et al.*, 1994). From the 326 genera

Table 1 *A priori* hypotheses (and rationale) of expected differences of trait categories between streams in mediterranean and temperate regions (note that this list includes only 31 [of the 61] categories for which we could provide such hypotheses, and that we viewed these categories as alternatives to cope with different climates, i.e. a given taxon may have only some of these traits). 'M' indicates that the category proportion should be higher in the mediterranean than in the temperate region, whereas 'T' indicates the contrary. Parts of the traits and their category labels used in Fig. 6 are indicated in bold (e.g. Maximum **size** ≤**2.5**)

Trait	Category		Rationale*
Maximum **size** (mm)	≤**2.5**	M	Better resilience capacity of smaller sizes after disturbances (i.e. floods or droughts)
	>**2.5–5**	M	(As above)
	>**5–10**	T	Release from disturbances requires less resilience capacity and permits larger sizes, but permanent action of flow forces (constraining large sizes) excludes very large sizes
	>**10–20**	T	(As above)
	>**20–40**	M	Release from action of flow in stagnant pools permits very large sizes
	>**40–80**	M	(As above)
Life cycle duration (yr)[†]	≤**1**	M	Better resilience capacity through shorter cycles after disturbances
Reproductive **cycles** (yr^{-1})[‡]	<**1**	T	Release from disturbances requires less resilience capacity and permits less-frequent reproduction
Aquatic **stages**	**Larva**	T	Riffles with permanent flow favour forms without aerial dispersal
	Imago	M	Stagnant pools favour forms with aerial dispersal (e.g. insects)
Reproduction	**Ovovivi**parity	M	Better resilience capacity through ovoviviparity after disturbances
	Terrestrial clutches	M	Increased resistance against droughts
	Asexual reproduction	M	Better resilience capacity through asexual reproduction (no need for sexual partner) after disturbances
Dispersal	**Aquatic passive**	T	Permanent action of flow forces increases downstream drift
	Aerial active	M	Flow cessation or bed dryness favour flying to other, less-dry sites
Resistance forms	**Refuge-use** against desiccation	M	Increased resistance against droughts
	Diapause or dormancy	M	(As above)
	None	T	Release from droughts requires no resistance forms
Locomotion and substrate relation	**Flier**	M	Flow cessation or bed dryness favour flying to other, less-dry sites
	Surface swimmer	M	Release from action of flow in stagnant pools permits swimming
	Swimmer	M	(As above)
	Crawler	T	Permanent action of flow forces imposes crawling
	Interstitial	M	Increased resistance against droughts (use of wetter space in substrata crevices as refuge)
Respiration technique	**Gills**	M	Higher temperatures and stagnant conditions make the oxygen uptake more difficult, i.e. specialized techniques (in comparison to simple tegument respiration) are required
	Plastron	M	(As above)
	Spiracle **(aerial)**	M	(As above)
Food	**Plant detritus** 1 mm	T	Response to more abundant and more nutritive litter input
	Living **microphytes**	M	Response to more-abundant periphyton algae
	Living **macrophytes**	M	Response to more-abundant macrophytes
Feeding habits	**Shredder**	T	Response to more abundant and more nutritive input of large litter
	Scraper	M	Response to more-abundant periphyton algae accessible by scraping

*The rationale was derived from predictions by Townsend & Hildrew (1994) on traits that favour resistance against or resilience from disturbances (adapted for temporary waters using Williams, 2001) and from major habitat differences between the regions: in comparison to temperate, typically permanently flowing streams, mediterranean streams have (1) more frequent and more severe disturbances by floods and droughts, (2) stagnant pools or dry beds during droughts, (3) overall higher temperatures, (4) less abundant and less nutritive allochthonous litter input from the riparian forest, and (5) higher primary production and plant biomass (periphyton algae and macrophytes); see Gasith & Resh (1999).
[†]Given that this trait had only one other category (>1), we predicted only on one category here.
[‡]Given that this trait had only two other categories (1, >1), we predicted only on one category here.
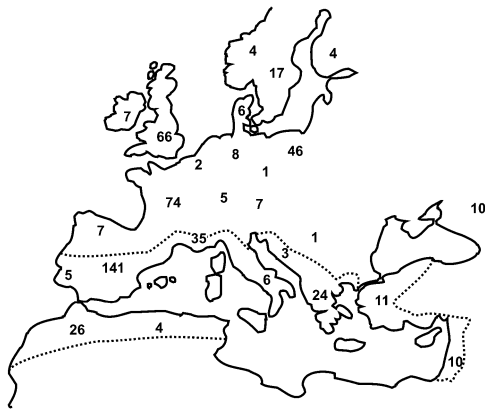
Fig. 1 Number and approximate location of sites and limit of the mediterranean climate (dotted lines) according to Köppen (1931).

analysed in this study, trait information for 14 genera from the mediterranean region (mostly Mollusca, Coleoptera, and Heteroptera) was unavailable in the database described by Statzner et al. (in press) and these were coded using published information, personal communications from experts, or by calculating a mean for genera within the same family.

Statistical analyses

Assessing the taxonomic and trait composition, we described regional and local taxonomic and trait richness, and local taxonomic and trait Simpson's (1-D) and Rao's diversity. Taxonomic and trait richness saturation was compared using accumulation curves (see e.g. Cao et al., 2001). Local trait richness was obtained using the number of different trait categories present at a site. Rao's quadratic diversity was computed using the Champely & Chessel (2002) index as developed by Pavoine & Dolédec (2005). This measures pairwise dissimilarities among species, which, when expressed in the form of a distance matrix, enables various diversity measures to be calculated according to the type of dissimilarity coefficient. This index can be applied to both taxonomic and trait matrices (e.g. Bady et al., 2005). We tested differences between regions for all variables using nonparametric Kruskal–Wallis tests.

We compared the taxonomic composition between the two regions using correspondence analysis (CA) on the log-transformed genus abundances. For characterization of the trait compositions, we multiplied the proportional affinity of the genera to each category per trait by the relative log-transformed genus abundances at the site. The resulting trait-by-site array contained the

relative abundance of each category per trait and site, which was analysed using fuzzy CA (FCA) (Chevenet et al., 1994). We assessed overall differences between regions in taxonomy and traits with between-class analysis, a particular case of multivariate analysis used for instrumental variables in which only one region serves as the instrumental variable (see Dolédec & Chessel, 1989; Lebreton et al., 1991). The significance of the overall difference (between-class variance) was tested against simulated values obtained after 1000 permutations of the rows of the taxonomic and trait-composition tables (Romesburg, 1985). We tested for differences along the first and second CA and FCA axes for regions and for each environmental characteristic using nonparametric Kruskal–Wallis tests.

For comparisons of the between-region variability of the taxonomic and trait composition, we considered an index of overall absolute variance as the sum of the eigenvalues of the between-class CA and FCA (with M and T as classes), which represented between-region variance. This allowed a direct comparison between taxonomic and trait variability. However, given that the amount of variability within a table is related to the number of variables and that the number of variables differed between taxonomic- and trait-composition tables (326 genera and 61 trait categories), we simulated taxonomic-composition matrices by randomly selecting 61 genera (i.e. the same number as trait categories) and recalculated the between-region variance. The distribution of 100 simulated values was then compared with the observed between-region variances obtained from the analysis of the entire taxonomic- and trait-composition arrays.

Finally, we tested for regional differences in the a priori-predicted individual trait categories (Table 1) using nonparametric Kruskal–Wallis tests. Statistics and graphical outputs were computed with the ADE4 library implemented in R freeware (Ihaka & Gentleman, 1996). The ADE4 library (see Thioulouse et al., 1997) can be freely obtained at http://pbil.univ-lyon1.fr/R/rplus/ade4dsR.html
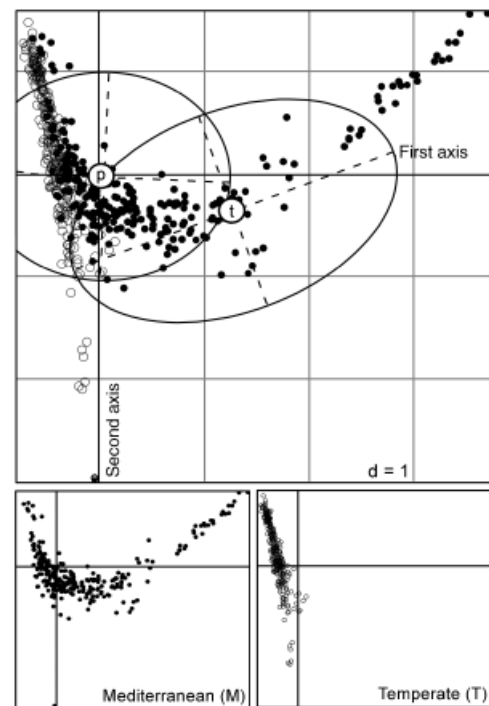
Results

Despite large differences in the area covered by both regions (T > M), regional taxonomic richness was higher in M (296 genera) than in T (224). Hundred genera were exclusive of M and 28 of T. All trait categories occurred in M and T. Local taxonomic richness and Simpson's and Rao's diversity were not significantly different between regions (Fig. 2a–c). Local trait richness and diversity were only slightly but significantly higher in M (Fig. 2e–g). Accumulation curves indicated that the
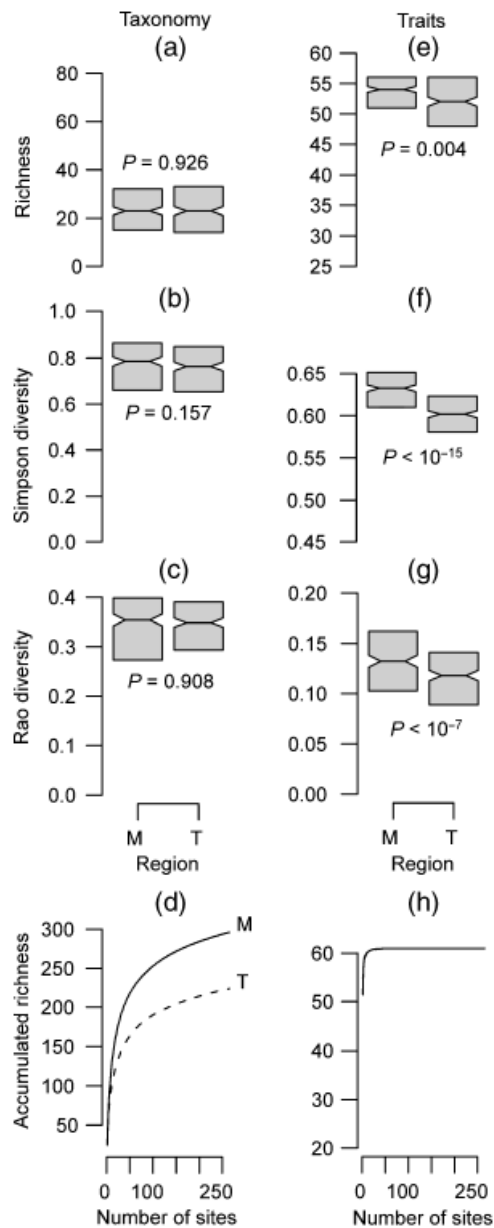
Fig. 2 Box-plots indicating local taxonomic and trait richness (a, e), local taxonomic and trait Simpson's (1-D) (b, f) and Rao's (c, g) diversity in M and T regions. The graphs show medians (horizontal bars), 25th and 75th percentiles (boxes), and *P*-values (obtained by Kruskal–Wallis tests). Taxonomic and trait-accumulation curves for the 326 genera and 61 trait categories, respectively, for 265 sites in each M and T are also presented (d, h).

Fig. 3 Correspondence Analysis (CA) of the log-transformed macroinvertebrate genus abundance at the 265 stream sites each in M (black circles) and T (open circles), with d indicating the scale of the graph. Ellipses envelop 70% of the sites with permanent (p) or temporary (t) flow conditions, the labels indicating the gravity centre of the ellipses. Bottom graphs display site distribution separated by region. Axes 1 and 2 explained 5.4% and 3.3% of the total variability, respectively.

taxonomic richness increased faster in M: with only 50 sites, M had about 100 more genera than T, suggesting a higher local taxonomic variability in M (Fig. 2d). Although these accumulation curves did not reach a plateau, the richness increase remained low above 200 sites. The trait–richness accumulation curves increased faster than the taxonomic ones, reaching a plateau with about 25 sites in both regions (Fig. 2h).

For genus abundances at the 530 sites, CA revealed a strong gradient along the first two axes (Fig. 3). Although many M-sites grouped with T-sites, many other M-sites differed in their taxonomic composition from T-sites so that the between-region difference was significant (between-class variance $= 0.299$, $P < 0.001$). M-sites had a higher variability and a different distribution along the first and second axes than T-sites. The first and second axis scores showed also a significant difference between regions ($P < 10^{-15}$ and $< 10^{-12}$, respectively). The gradient along the first axis related to the predominance of temporary and hard-water M-sites on its positive side (score medians of 1.10 and 0.27, respectively, $P < 10^{-15}$). M- and T-sites on the positive side of the second axis had predominantly high altitudes, permanent conditions, and soft waters (score medians of 0.8, 0.02, and 0.34, respectively, $P < 0.001$); large river sites predominated on the negative side of this axis (score median of -0.57, $P < 10^{-4}$). Between-region differences remained after hardness effects were
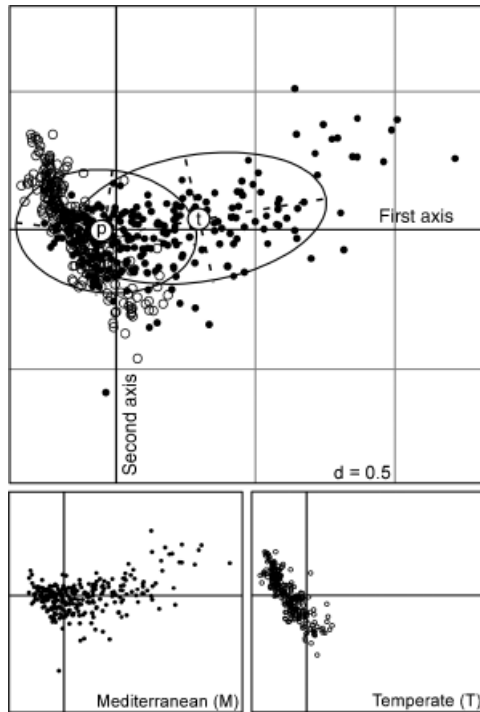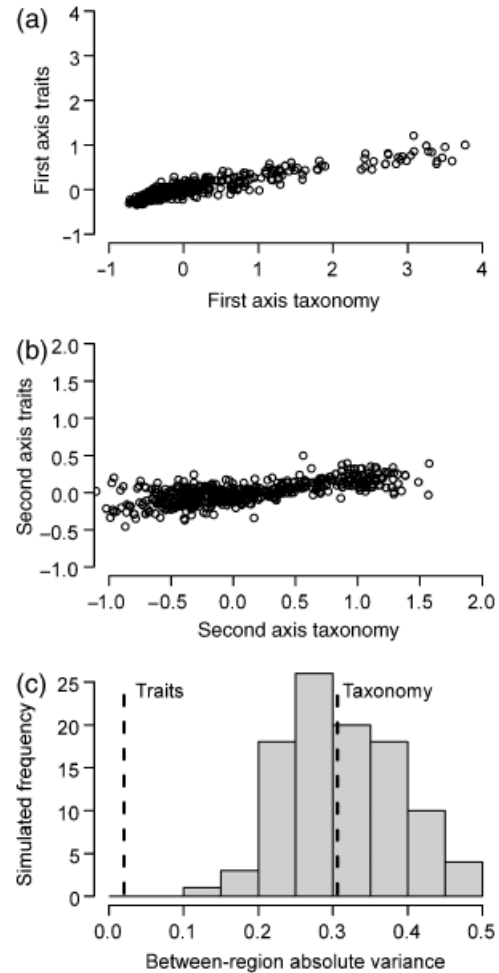
Fig. 4 Fuzzy Correspondence Analysis (FCA) of the relative abundance of the biological trait categories of macroinvertebrates at the 265 stream sites each in M (black circles) and T (open circles). Axes 1 and 2 explained 32.2% and 10.9% of the total variability, respectively. See Fig. 3 for further details.

Fig. 5 Site scores along the first (a) and second (b) axes of the CA (for the taxonomic composition) plotted against those of the FCA (for the trait composition) (see Figs 3 and 4), and observed (broken lines) and frequency of 100 simulated values (for 61 randomly selected genera, corresponding to the number of the 61 trait categories) of the absolute between-region variance for the taxonomic and trait composition (c).

removed using the residual values of the relationship between hardness and the first CA axis ($P < 10^{-15}$) (i.e. these differences related still to the predominance of temporary sites in M; Fig. 3).

Similar to the analysis of the taxonomic composition, FCA on all trait categories indicated a strong site gradient, especially along the first axis (Fig. 4). M-sites had a higher variability and were more distributed along the first axis than T-sites. Although T-sites grouped with M-sites on the negative first-axis side, trait composition significantly differed between regions (between-class variance = 0.021, $P < 0.001$). Regional differences were significant for the first ($P < 10^{-15}$) but not for the second-axis scores ($P = 0.364$). Sites on both sides of the first axis were associated with the same environmental variables as in the taxonomic composition analysis, and significant between-region differences again remained after removing hardness effects ($P < 10^{-15}$). Thus, regional trait differences were also related to the high predominance of temporary sites in M (Fig. 4).

Although significant differences between regions appeared for the taxonomic and trait composition, the site scores on both axes in Figs 3 and 4 suggested that variability was higher in taxonomic than in trait analysis. This was supported by plots of the trait vs. taxonomic site scores (Fig. 5a,b). Simulating between-region variances with randomly selected 61 genera (equalling the number of trait categories) confirmed statistically that the taxonomic composition was more variable between regions than the trait composition: all 100 simulated taxonomic values were higher (i.e. $P < 0.01$) than the observed value for the trait composition (Fig. 5c). In addition, the observed between-region taxonomic variance including all 326 genera and most of the simulated taxonomic values were about 10 times higher than the observed between-region trait variance (Fig. 5c).
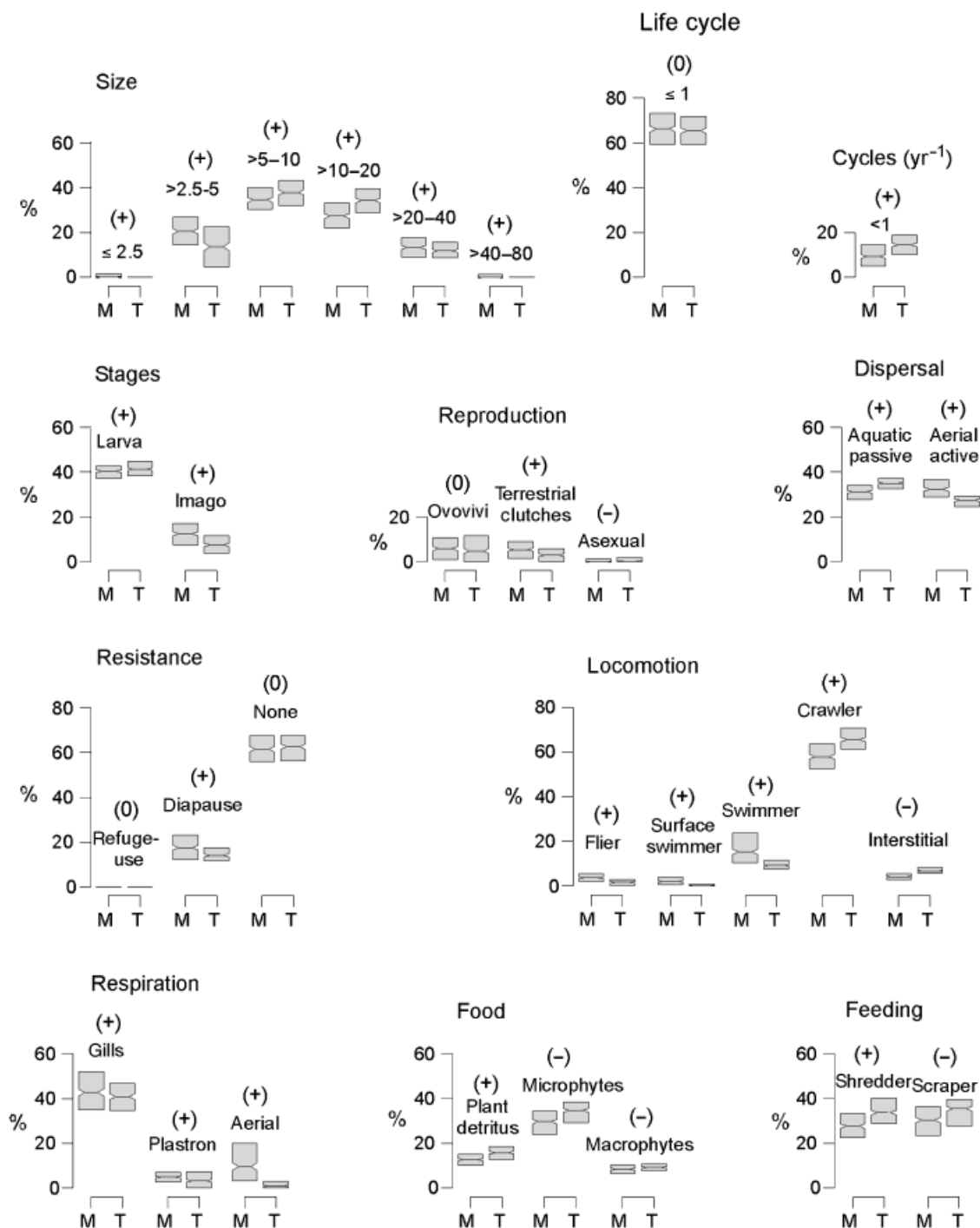
Fig. 6 Box-plots indicating the proportion (in %) of categories per trait for *a priori* predicted differences in 31 trait categories between M and T (Table 1). Recall that the traits had more categories (overall 30) for which we could not provide *a priori* predictions. For each trait category, (+) indicates a significant match with the prediction, (−) a significant mismatch, and (0) that no significant differences were found. Except for the ">20–40", "gills", and "plastron" categories ($P < 0.05$), all others that significantly differed (after applying Bonferroni correction) had *P*-values between $P < 0.002$ and $< 10^{-15}$. See Table 1 and Fig. 2 for further details.

From the *a priori* hypotheses (Table 1) on between-region differences in 31 trait categories, 22 were significantly confirmed (19 after Bonferroni correction), five significantly contradicted, and four did not differ significantly between regions (Fig. 6). For the traits maximum size, reproduction cycles per year, aquatic

stages, dispersal, and respiration, all category predictions corresponded to the observed differences, whereas for most of the other traits, at least some of the category predictions corresponded. Compared with T-sites, M-sites had more macroinvertebrates with small size, aquatic imagines, aerial active dispersal, swimming locomotion, or aerial respiration. In contrast, T-sites had more macroinvertebrates with intermediate size, aquatic larvae, aquatic passive dispersal, or crawling locomotion. In addition, T-sites had more macroinvertebrates having less reproductive cycles per year and shredders of coarse detritus or scrapers of microphytes (Fig. 6). Overall, however, the quantitative differences of the median values between M and T were relatively small (<15 percentage points) for most categories.

Discussion

Actual ecological differences between regions

Higher regional genus richness in M than in T confirmed our first hypothesis, similar to observations on terrestrial plants (Raven, 1973; Deacon, 1983). This could be explained by geological events (e.g. glaciations caused higher speciation in southern regions and taxonomic losses in northern regions; Ribera & Vogler, 2004). Thus, M-streams are biodiversity hotspots for macroinvertebrates, particularly because the higher regional richness in M occurred in a smaller area if compared with the area of T. Contrary to our second hypothesis, we found no regional differences for local (site) taxa richness and diversity, indicating regulation by local environmental characteristics (Ricklefs, 1987). Consequently, high among-site environmental heterogeneity caused higher mediterranean richness. Obviously, the spatial and temporal heterogeneity is high in M, where many stream types differ in flow conditions, geology, main water source (e.g. Munné & Prat, 2004), and the relative importance of habitats such as riffles and pools in winter or summer (Gasith & Resh, 1999). Despite similar local taxonomic richness and diversity in M and T, local trait richness and diversity were significantly (though only slightly) higher in M, indicating that the genera at M-sites differed more in their functional roles, perhaps because the higher seasonality in M caused more temporal trait variability.

Many M-sites had a taxonomic and trait community composition similar to T-sites, as we considered climate at the macroscale. Thus, M included high mountain streams with low temperatures and low seasonal flow variability (having similar conditions as T-sites) (Bonada et al., 2002). Nevertheless, local taxonomic and trait composition differed significantly between regions,

supporting our third and fourth hypotheses. These differences might be related to historical or actual ecological factors. For example, glaciations during the Pleistocene caused an exceptional speciation of some insect orders in M (e.g. aquatic Coleoptera, see Ribera & Vogler, 2004), and among these new taxa many succeeded in M because of traits adapted to mediterranean climate. Among the ecological factors differing between M- and T-sites, geology (mainly calcareous and karstic in M, see Grove & Rackham, 2001), and thus, water hardness were strongly associated with the observed differences in community composition. Geology clearly discriminates macroinvertebrate communities in large-scale studies (Verdonschot & Nijboer, 2004), and particular species characterize calcareous, siliceous, and sedimentary stream reaches (Bonada et al., 2005). However, at large spatial scales, macroinvertebrate variability should also be related to climatic characteristics (Poff & Ward, 1990). Although not independent from local geology and other ecosystem aspects, climatic conditions obviously influence temporality (Smith et al., 2003). Thus, removing geology effects using the residuals of the water hardness relations, significant differences between M and T for the local taxonomic and trait composition persisted and were, thus, associated with a higher frequency of temporary M-sites. Regarding their taxonomic composition, permanent sites, having riffle-pool sequences along the year, are characterized by the dominance of Ephemeroptera, Plecoptera, and Trichoptera; if sites are temporary and pools prevail during droughts, Odonata, Coleoptera, and Heteroptera dominate (e.g. Boulton & Suter, 1986; Bonada et al., 2006a). Correspondingly, Plecoptera ($P < 10^{-15}$) and Trichoptera ($P < 10^{-9}$) had a higher local genus richness in T- than in M-sites, whereas Odonata ($P < 10^{-15}$), Coleoptera ($P < 10^{-11}$), and Heteroptera ($P < 10^{-15}$) were richer in M-sites. Only Ephemeroptera, having some lentic warmwater genera (e.g. *Caenis*; Perán et al., 1999), had a similar richness ($P = 0.943$) in M- and T-sites.

Standardized between-region variability was 10 times lower for the traits (Fig. 5c), supporting our fifth hypothesis. The trait composition of communities should be less variable across geographical areas than their taxonomic composition (Charvet et al., 2000; Hausner et al., 2003), because the traits aggregate biological information shared among different taxa. Correspondingly, Statzner et al. (2001a, 2004, 2005) reported relatively high invertebrate trait stability across European streams and large rivers, which was presumably caused by similar local conditions (i.e. similar physical flow harshness) that predominated compared with other large-scale factors (e.g. climatic differences across Europe).

Given that we viewed our 31 *a priori* trait predictions as alternatives to cope with mediterranean or temperate

climates (Table 1), significant support of 22 predictions suggested confirmation of our sixth hypothesis. However, we admit that some of the trait categories differing between M and T should be related. For example, small-sized organisms reproduce typically more frequently.

Mediterranean ecosystems have a remarkable capability of resisting against or to recover from disturbances in comparison with nonmediterranean ones (Fox & Fox, 1986). Correspondingly, M-sites had more macroinvertebrates (than T-sites) with traits providing better resistance against droughts (reproduction through terrestrial clutches, summer diapause, specialized respiration techniques) and better resilience after droughts or other disturbances (small body size, more frequent reproduction, aerial active dispersal as fliers, all favouring dispersion and rapid recolonization of disturbed stream sites). In addition, the higher relative abundance of other trait categories in M-sites related to stagnant pool conditions as predicted (very large size, aquatic imagines, swimming locomotion). Unexpectedly, asexual reproduction was more abundant in T- than in M-sites, probably because of the higher abundance of coldwater Tricladida in T-sites (e.g. mean *Crenobia* abundance in T was about ten times higher than in M). We only partly confirmed our *a priori* hypotheses for food and feeding traits. As expected, shredders of coarse detritus were more abundant in T-sites, but unexpectedly scrapers of periphyton and microphytes were less abundant in M-sites. Thus, although M-sites have generally a higher periphyton production and biomass (Velasco *et al.*, 2003; Giorgi *et al.*, 2005), other factors should have limited scraper abundance in M-sites. Predators can control scraper production (Stagliano & Whiles, 2002), and in mediterranean streams predation is very important in summer when periphyton has its maximum production (Gasith & Resh, 1999). However, other factors, such as autumn and winter floods, could have also limited scrapers in M-sites, and we have no unequivocal explanation for this and other trait patterns that did not correspond to our predictions.

Although the differences in trait-category patterns between M and T were often highly significant, they were relatively weak in terms of quantities, as the median values of the category proportions differed typically by less than 15 percentage points between M and T (see Fig. 6). Correspondingly, Statzner *et al.* (2004) reported weak quantitative (but significant) differences in macroinvertebrate traits for predominantly temperate European stream sites differing in altitude or stream width. Overall, however, Statzner *et al.* (2004) found ecologically meaningful and significant trait differences between such environmental conditions for fewer categories than us. Thus, our analysis of a ba-lanced number of M- and T-sites showed that, although the quantitative differences were similarly weak, more trait categories differed ecologically meaningful and significantly between M and T than across altitudinal or stream size gradients of predominantly temperate streams.

Implications of climate change for stream macroinvertebrate communities

Deriving implications of climatic change from our analyses, we had three major concerns. First, our macroinvertebrate abundance data covered ~40 years in both regions (1961–2004, with only two T-sites assessed earlier), hence part of the data variability (particularly in T) might already be due to climate change (potentially decreasing differences between M and T). However, although cold-water macroinvertebrates decreased in abundance in T-headwaters over the last 20 years (Daufresne *et al.*, 2004), the latter did not disappear from the area (www.faunaeur.org). Furthermore, the regional differences in macroinvertebrate patterns were primarily related to higher drought frequency in M, and droughts did not become more frequent in Europe since the 1930s (Hisdal *et al.*, 2001). Second, using fuzzy coding in trait analyses could have limited the detection of subtle effects of climate change, as fuzzy coding captures within-genus phenotypic plasticity across species. Third, using spatial differences (M vs. T) provided only an approximation to anticipate ecological responses to climate change. Ideally, models predicting taxa and trait loss, contraction, and expansion should be developed (e.g. Bakkenes *et al.*, 2002) (i.e. our approximation indicated only general trends of climate change implications).

Several authors argued that changes in structural patterns due to climate change would have strong functional consequences (Bakkenes *et al.*, 2002; Peterson *et al.*, 2002), but most studies indicating that climatic change affected structure and function in terrestrial ecosystems considered only few species (e.g. Walther *et al.*, 2002). Our findings and climate forecasting for Europe suggest that (1) macroinvertebrate communities in T would change in structural (taxonomic) and functional (trait) composition, (2) structural changes would be greater than functional changes, and (3) on average, local structural and functional richness and diversity would be scarcely affected.

If T-streams become more temporary because of droughts, we anticipate that macroinvertebrates actually characterizing M would increase in T. Organisms have two possibilities to respond to such changing environmental conditions: either changing their distribution or adapting, and the strategy to cope with new

conditions depends on the phenotypic trait plasticity. Unlikely, a caddisfly cementing its eggs on stones in riffles would change to terrestrial oviposition if streams become too dry (i.e. its distribution would change). However, a mayfly with a univoltine life-cycle would likely become multivoltine, thus adapting to temperature increases (Perán et al., 1999). For terrestrial species it is expected that most of them would change their distribution if climate changes (Bakkenes et al., 2002; Hickling et al., 2005), but adaptation through changing phenology is also likely (Bradley et al., 1999; Both & Visser, 2005). Our results suggest that M-macroinvertebrates with their higher dispersion and colonization capability would immigrate into actual T-sites, whereas T-macroinvertebrates would move northwards (contracting their ranges) or perhaps adapt to the new climate. Northward migration of T-macroinvertebrates would imply the local extinction of taxa in their actual range area (Bakkenes et al., 2002; Erasmus et al., 2002), which could have strong implications for the local taxonomic conservation, but only weak implications for the trait diversity and composition of communities.

Beyond T, climate change expectedly would exacerbate summer droughts (Gibelin & Déqué, 2003) and the species loss in M (Bakkenes et al., 2002). Temporary stream sites would become more frequent in M and likely some macroinvertebrate taxa actually inhabiting permanent streams would disappear or emigrate to permanent springs, because of direct or indirect (less dilution of pollution) effects of discharge reductions (Mulholland et al., 1997; Eckhardt & Ulbrich, 2003). However, in highly heterogeneous regions such as the Mediterranean Basin (Grove & Rackham, 2001), populations have perhaps a higher genetic polymorphism or higher phenotypic plasticity than elsewhere (Schlichting, 1986; Nylin & Gotthard, 1998), which would help them cope with climate change and maintain mediterranean biodiversity.

Currently, several approaches are discussed to indicate ecological effects of climate change in stream communities (e.g. www.eurolimpacs.ucl.ac.uk). Among them, a biological-trait approach would provide three major advantages compared with, for example, a taxonomic approach: (1) traits aggregate all taxa in fewer functional categories, simplifying a priori predictions (Pausas et al., 2004; Statzner et al., 2005; this study), (2) abiotic variables, among them climate, filter primarily for traits and only in turn for taxa (Poff, 1997; Statzner et al., 2004; this study), and (3) trait changes would indicate functional community and thus ecosystem changes (Statzner et al., 2004; Bonada et al., 2006b; this study). Related to the objective to achieve sustainable development, functional community characteristics are obviously more important than taxonomic ones, whereas the latter relate more to the objective of taxonomic conservation. For macroinvertebrate traits and European streams, we anticipate that climate change would cause changes in functional community characteristics that would be statistically highly significant but rather weak in terms of quantities.

Acknowledgements

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