



Spatial autocorrelation patterns of stream invertebrates: exogenous and endogenous factors

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ABSTRACT

Aim To investigate spatial autocorrelation of taxonomic stream invertebrate groups (richness and composition) at a large geographical scale and to analyse the importance of exogenous and endogenous factors.

Location The Mediterranean Basin.

Methods For exogenous factors, we used large-scale factors related to climate, geology and river zonation; for endogenous factors, we used the dispersal mode of each taxonomic group. After describing and analysing spatial patterns of genus richness and genus composition of stream invertebrate groups in the Mediterranean Basin, we computed Moran's *I* before and after accounting for the exogenous factors and related it to the endogenous factors.

Results In relation to genus richness, most of the taxonomic groups did not show significant spatial autocorrelation, suggesting that no main large-scale exogenous or endogenous factors were important and that local-scale factors were probably controlling taxonomic richness. In contrast, for genus composition, all taxonomic groups except Odonata had significant spatial autocorrelation before accounting for the environment. After accounting for the environment, most taxonomic groups still had a significant spatial autocorrelation, but it decreased with their increasing dispersal ability (from Crustacea to Coleoptera). Thus, spatial taxonomic composition of groups with the strongest dispersal potential is mainly related to exogenous factors, whereas that of groups with weaker dispersal potential is related to a combination of exogenous and endogenous factors.

Main conclusions Our results illustrate the importance of dispersal as an endogenous factor causing spatial autocorrelation and suggest that ignoring endogenous factors can lead to misunderstandings when explaining large-scale community patterns.

Keywords

Dispersal, genus richness, invertebrates, Mediterranean Basin, Moran's *I*, spatial autocorrelation, streams, taxonomic composition.

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INTRODUCTION

Typically, the world is spatially and temporally autocorrelated, and the lack of attention to this in classical statistical analysis is a potential source of misleading results in ecological and biogeographical analyses (Legendre, 1993; Koenig, 1999). Spatial autocorrelation (SAC) refers to the concept that environmental or biological values observed at a given site are not independent of values at more or less distant neighbouring sites, resulting in

patches or gradients (e.g. Thioulouse *et al.*, 1995). While the spatial pattern of a distribution refers to the geographical arrangement of entities, SAC provides a measure of the relevance of this spatial pattern (i.e. how the influence among adjacent areas causes general spatial patterns; Chou, 1995). When referring to properties of populations or communities, SAC can be caused by autocorrelated exogenous factors or by endogenous factors interfering with spatial patterns (Koenig, 1999; Kendall *et al.*, 2000; Liebhold *et al.*, 2004).

Exogenous factors control the occurrence and abundance of organisms through their action on ecological niches (e.g. the presence of a suitable habitat). These external factors are generally related to environmental variables operating at multiple spatial and temporal scales (Heino *et al.*, 2007). For example, in large spatial analyses, temperature and rainfall are usually spatially autocorrelated and it is relatively common to find organisms matching these environmental patterns (Koenig, 1999, 2002; Lennon, 2000). In contrast, endogenous factors are those biological traits of organisms acquired through the evolution of morphological or behavioural characteristics, such as feeding strategies, reproduction type, migration, life cycle, gregarious behaviour or dispersal characteristics. For example, a positive SAC is observed in plants with vegetative reproduction, limited seed dispersal or specific types of growth, and in the animal world related to certain migration patterns in connection with the search for prey or areas for reproduction (Ims & Steen, 1990; Miller *et al.*, 2002). Some endogenous factors are, however, not totally independent of exogenous factors; for example, the dispersal ability of organisms can be constrained by landscape configurations (Keitt, 1997; Bohonak & Jenkins, 2003). Both types of factors have long been recognized to constrain the presence of organisms in a habitat (Thienemann, 1918), but they are rarely considered together.

Using specific statistics, ecologists try to reduce SAC in their data before classical statistical analysis (Lennon, 2000; Diniz-Filho *et al.*, 2003). Ongoing developments also address multiple scale pattern analysis (Jombart *et al.*, 2009) for modelling of spatial variation on different scales. However, very few studies have analysed the causes of SAC and even fewer have considered the role of endogenous factors, which can be more difficult to quantify than exogenous ones (Dormann, 2007; Shurin *et al.*, 2009). Theoretical studies focusing on population dynamics have demonstrated that exogenous and endogenous factors should be considered together to explain, and therefore to reduce, SAC (Kendall *et al.*, 2000; North & Ovaskainen, 2007). The few empirical studies considering endogenous factors so far at the population and community level suggest that they play an important role in SAC (Smouse & Peakall, 1999; Dirnböck & Dullinger, 2004; Shurin *et al.*, 2009).

Studies of SAC at the population level typically include spatial descriptions of abundance patterns and their dynamics, whereas such studies at the community level have often focused on taxonomic richness and have rarely included other community properties (e.g. Liebhold *et al.*, 2004; Briers & Biggs, 2005; Tedesco *et al.*, 2005). Thus, very few studies have considered community composition in SAC analysis (see Grenouillet *et al.*, 2004), and even fewer have addressed the factors explaining the SAC of community composition (Briers & Biggs, 2005). This contrasts with the numerous studies on the spatial patterns of communities and related exogenous factors (e.g. Borcard & Legendre, 1994; Weigel *et al.*, 2003; Sandin & Johnson, 2004; Jombart *et al.*, 2009). Beyond its theoretical importance, the analysis of the SAC of community

properties and the factors ruling it can also have implications for conservation issues; for example, SAC could be used in conservation management to detect spatial discontinuities of communities.

Our goal is to investigate the SAC of stream invertebrate communities (richness and composition at the genus level) at a very large scale (the Mediterranean Basin) and to assess the importance of exogenous and endogenous factors. We opted for the use of stream invertebrates because of their response to multiple environmental conditions and the amount of information found on several endogenous factors potentially important for SAC (e.g. a great variety of biological trait categories have been described for them; Tachet *et al.*, 2002). As exogenous factors, we use large-scale factors related to climate, geology and river zonation because these factors have significant effects on invertebrate communities across large spatial scales (e.g. Verdonschot & Nijboer, 2004). As endogenous factors, we focus on dispersal mechanisms because the ability of species to reach a remote stream site should be relevant for the understanding of large spatial patterns of species assemblage in communities. We hypothesized that the spatial patterns of taxa with the strongest dispersal potential (i.e. those with a predominantly aerial active dispersal) should be found to be related only to exogenous factors because they can easily reach all sites. In contrast, spatial patterns of taxa with the weakest dispersal potential should be related to a combination of exogenous factors and the dispersal itself (i.e. the endogenous factor). We also hypothesized that these assumptions should be better supported through analyses of community composition than through observations of taxonomic richness, because the latter is a simplified description of community complexity and does not reflect taxon identity. In addition, taxonomic richness has much stronger dependence on methodology/sampling intensity than taxonomic composition.

MATERIALS AND METHODS

Site location and biological data

The study area comprised a region of about 1,100,000 km² (Grove & Rackham, 2001) in the Mediterranean Basin with a mediterranean climate according to the Köppen classification system (Köppen, 1931). This area is characterized by hot, dry summers and cool, wet winters. Mean summer and winter temperatures range from 14 to 25 °C and from 7 to 13 °C, respectively. Mean annual rainfall ranges from 275 to 900 mm (Paskoff, 1973). Streams in this region have predictable seasonal droughts and floods. For stream invertebrates, as well as vertebrates and plants (Myers *et al.*, 2000), this area has been considered a biodiversity hotspot that differs from adjacent climatic areas in terms of taxonomic and functional composition of communities (Bonada *et al.*, 2007).

We used biological data from 265 stream sites in the mediterranean climate area assembled by Statzner *et al.* (2007) and Bonada *et al.* (2007) and complemented these sources

with data from 223 additional sites from Herbst & Mienis (1985), Moubayed (1986), Muñoz *et al.* (1986), Carchini *et al.* (1988), Bouzidi (1989), Tuch & Gasith (1989), Vidal-Abarca *et al.* (1991), Degani *et al.* (1992), Provini *et al.* (1993), Ferrito (1994), Fochetti *et al.* (1994, 1998, 2000), Nicolai *et al.* (1996), Kazanci *et al.* (1997), Guerrero *et al.* (1998), Talami (1998), Vourdoumpa (1999), Lounaci *et al.* (2000), Faure (2003) and Ortiz *et al.* (2005). Information on the presence/absence of stream invertebrate genera was available for the 488 sites; these sites were classified as least impacted stream reaches according to the criteria described in Statzner *et al.* (2007).

To analyse the spatial pattern of our data, we considered spatial units of 1° longitude and latitude following Littmann (2000, fig. 3 therein) and assigned sites to each spatial unit. These spatial units are large enough to summarize local spatial variability and small enough to allow the detection of spatial changes on a large-scale. Spatial units were used instead of individual sampling sites because sites were not uniformly distributed (i.e. some datasets included many sites within a single basin, whereas others included only one site per basin). Littmann's map covers an area between 7° W and 37° E and 45° to 30° N, which has 660 spatial units. Given that our 488 sites were irregularly distributed across 57 spatial units (Fig. 1a), we only selected those spatial units having data for ≥ 3 sites. This arbitrary choice was a compromise between statistical power and data availability. For spatial units having more than three sites, we randomly selected three sites and finally included a total of 117 sites associated with 39 spatial units (Fig. 1a). Given that these data were collected using different methodologies and devices, the effects of sampling

method (kick, surber-core, others) and mesh size (very small, small, large) on the richness were analysed for each taxonomic group using one-way ANOVA. First, the effect of environmental variability (elevation, water hardness, river size) was partialled out and the residuals were used to perform one-way ANOVA. Due to heterogeneity in data information, we could analyse only 108 sites for sampling and 76 sites for mesh size. The only significant effect of sampling method occurred in Mollusca genus richness, which represented 7.7% of all variability ($P = 0.014$). Mesh size had a higher effect than sampling method and was significant for Plecoptera ($R^2 = 28.4\%$, $P < 0.001$), Trichoptera ($R^2 = 14.6\%$, $P < 0.0035$), Crustacea ($R^2 = 10.3\%$, $P < 0.0025$) and Ephemeroptera ($R^2 = 9.8\%$, $P < 0.0025$) genus richness. In addition, the effect of sampling method and mesh size was analysed on the presence/absence composition table using partial redundancy analysis (ter Braak, 1988). The statistical significance of the effect of sampling method or mesh size was assessed by a Monte Carlo test ($n = 999$ random permutations) on the percentage of variability explained by sampling or mesh size. Sampling method and mesh size had a significant but low effect on the invertebrate composition (14.6%, $P = 0.001$ and 17.7%, $P = 0.001$, respectively). Therefore, with the exception of Plecoptera, methodological variability within our metadataset had significant but low influence on explaining invertebrate patterns. These low influences of the methodological characteristics on Plecoptera were potentially spatially autocorrelated (see Statzner *et al.*, 2004), although varying methods such as kick and surber sampling using different mesh sizes were all used in the Iberian Peninsula, from whence the majority of data were included in this study. For more characteristics of the methods used to build this metadataset, see Statzner *et al.* (2007).

Exogenous factors

To assess whether the spatial pattern of stream invertebrates was associated with spatially autocorrelated environmental variables, most large-scale variables relevant for these organisms were used for each site (Verdonschot & Nijboer, 2004). Elevation (lowlands, highlands and mountains for < 150 , 150–1000 and > 1000 m a.s.l., respectively), water hardness as a surrogate for geology (soft, intermediate and hard for < 200 , 200–400 and $> 400 \mu\text{S cm}^{-1}$, respectively) and river size (small, intermediate and large for < 10 , 10–40 and > 40 m width, respectively) were obtained from the original literature used. Furthermore, we included values of mean annual rainfall and mean annual air temperature from the closest meteorological station of each selected site (Walter & Lieth, 1967).

Endogenous factors

To assess the influence of endogenous factors on the spatial pattern of our stream invertebrates, we could use a wide variety of morphological or behavioural characteristics. However, not all endogenous factors should be a priori relevant in large-scale

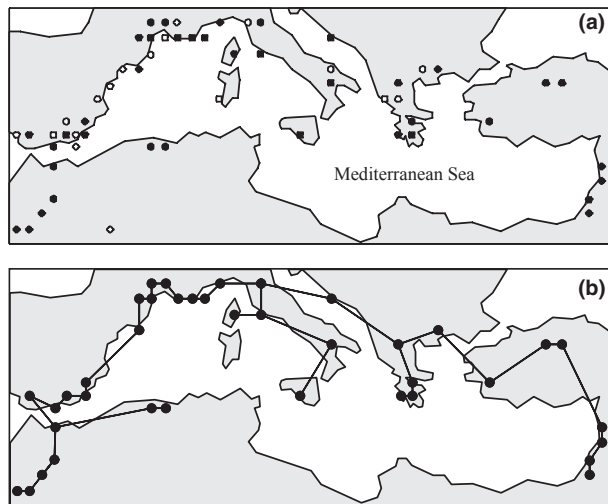


Figure 1 (a) Location of the 57 spatial units in the Mediterranean Basin, according to Littmann's (2000) classification, for which data on stream invertebrates were available. Black dots indicate the 39 spatial units with ≥ 3 sites that we used in our analyses, whereas white dots indicate units with < 3 sites (i.e. not used in our analyses). (b) Location of the 39 selected spatial units with a line joining them by considering the shortest path according to several criteria (see text).

studies such as ours. For example, some endogenous factors that are related to biotic interactions (e.g. being a predator or a parasite) can be important to explaining local-scale spatial patterns of abundance, richness or composition; however, such factors rarely affect large-scale spatial structures (Guisan & Thuiller, 2005). Likewise, a type of reproduction producing numerous offspring has no large-scale implications if the offspring cannot disperse. Because dispersal has been considered the most obvious endogenous factor at multiple spatial scales (e.g. Dormann, 2007), we used dispersal traits as a variable to assess large-scale spatial patterns of our stream invertebrate communities.

Across large spatial scales, knowledge of traits favouring overland or long-distance dispersal should improve the understanding of spatial patterns of organism distributions (Nathan *et al.*, 2003). Among stream invertebrates, dispersal has been described by four categories depending on the medium used and the dispersal mechanism (Tachet *et al.*, 2002; Bohonak & Jenkins, 2003): 'aquatic passive', 'aquatic active', 'aerial passive' and 'aerial active'. Aquatic passive dispersal refers to downstream movements of individuals by drift, a topic that has been repeatedly studied (e.g. Bilton *et al.*, 2001; Elliot, 2002). Drift is a very common phenomenon in running waters and it is one that has evolutionary implications (i.e. organisms have developed morphological and behavioural strategies to cope with drift; Brittain & Eikeland, 1988; Oberto *et al.*, 2004). Obviously, drift does not provide overland dispersal as occurs during aquatic active dispersal. The latter form of dispersal enables invertebrates to move actively through river networks by crawling or swimming upstream or downstream. Aerial passive dispersal provides overland displacement of individuals by wind (of winged adults or diapause forms) or by terrestrial vertebrates (i.e. by birds). However, dispersal by this type, even if poorly understood, is considered limited (Bohonak & Jenkins, 2003). **Finally, aerial active dispersal of terrestrial stages with wings has been widely documented, showing that some stream invertebrates can travel overland for tens of kilometres (Wikelski *et al.*, 2006).**

Dispersal abilities of stream invertebrates are difficult to measure. Direct measures with traps have been traditionally used but they are not feasible across large spatial scales (Petersen *et al.*, 1999). More recently, indirect measures related to genetic analyses of single or few species were used across various spatial scales (Nathan *et al.*, 2003). However, genetic analyses are unavailable for most species and other methods have to be used to analyse community patterns instead. One possibility is to use other indirect measures that provide summary information about the ability of each taxon to disperse according to the four categories explained above. This analysis is based on invertebrate morphology (e.g. presence of winged adults) or on empirical results (e.g. ability to drift downstream). Using this kind of information, provided by Tachet *et al.* (2002), we calculated a dispersal index for each taxonomic group included in our study (i.e. Mollusca, Crustacea, Ephemeroptera, Plecoptera, Odonata, Trichoptera, Heteroptera and Coleoptera) based on the degree of affinity of

each genus to each of the four dispersal categories. This degree of affinity is described using a fuzzy coding approach (Chevenet *et al.*, 1994) and includes all the available information in Europe during the 20th century. For example, the Odonata genus *Anax* is coded as 0/1/0/3 for the categories 'aquatic passive'/'aquatic active'/'aerial passive'/'aerial active', which indicates that it has a dominant aerial active, a weak aquatic active and no passive dispersal (Tachet *et al.*, 2002). To compute a dispersal index, the affinity values for each genus were standardized to sum to 1 (i.e. resulting in 0/0.25/0/0.75 for *Anax*) and arbitrarily weighted according to the potential relevance of aquatic or overland dispersal for the SAC explained above (i.e. the ability to have long-distance overland dispersal; Nathan *et al.*, 2003). Thus, 'aquatic passive' was weighted by 1, 'aquatic active' by 5, 'aerial passive' by 10 and 'aerial active' by 20 (i.e. resulting in 0/1.25/0/15 for *Anax*). Finally we added these weighted values (i.e. resulting in a value of 16.25 for *Anax*) and computed the mean using the values of all genera within each larger taxonomic group. A taxonomic group with a high dispersal index would have high dispersal abilities across larger spatial scales, whereas a group with a low dispersal index would have limited dispersal abilities. According to our hypothesis, groups with low dispersal indices should show significant SAC even after accounting for the environmental variables. Additionally, we also computed the mean affinity value for each dispersal category and taxonomic group.

Statistical analyses

To investigate SAC, we established a neighbouring graph (Fig. 1b; Thioulouse *et al.*, 1995 and references therein) from a spatial matrix that contained as many rows and columns as the number of spatial units, assigning a value of '1' if two spatial units are neighbours among the 39 units and '0' for 'otherwise' in the *i*th row and the *j*th column of the matrix. We linked a site to its immediate nearest neighbours for computing distances among spatial units as the length of the shortest path between spatial units (using coordinates of latitude and longitude). We corrected this automatic selection by considering three criteria: (1) Tunisian spatial units were considered closer to Morocco than to Spain because the shortest distance across the Mediterranean Sea is through the Strait of Gibraltar; (2) southern Spain spatial units were considered closer to northern Spain than to Tunisian spatial units because dispersal over land is more probable than over the sea; and (3) similarly, Croatian spatial units were considered closer to Greek than to southern Italian spatial units (Fig. 1b).

We used Moran's *I* (1950) statistics (Cliff & Ord, 1973) for the quantification of SAC:

$$I = \frac{n \sum_{i,j=1; i \neq j}^n w_{ij} z_i z_j}{\sum_{i,j=1; i \neq j}^n w_{ij} \sum_{i=1}^n z_i^2 / n}$$

where *n* is the number of observation sites and **W** the row standardized matrix of spatial weights (w_{ij}), x_i and x_j are the values of the observed variable at site *i* and *j*, respectively, and

$z_i = x_i - \bar{x}$ and $z_j = x_j - \bar{x}$. Positive and significant Moran's I values mean that nearby areas have similar spatial patterns, whereas negative values indicate the contrary. We computed global Moran's I for environmental variables to describe their spatial patterns.

For analyses of taxonomic richness, we calculated mean genus richness of each taxonomic group in each spatial unit. For analyses of taxonomic composition, we used the entire composition of each taxonomic group in each spatial unit to perform a principal components analysis (PCA) on the data. To analyse the influence of exogenous factors on the observed biotic patterns, we used general linear modelling (GLM) for genus richness in each taxonomic group and selected models according to the small sample unbiased Akaike's information criterion (AIC_c) (see, e.g., Burnham & Anderson, 2002). For the taxonomic composition, we used redundancy analysis (RDA, see, e.g., Legendre & Legendre, 1998) to search for linear combinations of environmental variables that explain genus composition of each taxonomic group. We tested the significance of the overall explained variability (sum of all eigenvalues of the RDA) of each taxonomic group by environmental variables using a permutation test (999 runs).

We checked for SAC in the invertebrate data, computing global Moran's I before and after accounting for environmental variables. The effect of SAC on genus richness after accounting for the environment was computed using the residuals from previously computed linear multiple regressions. The effect of SAC on taxonomic composition before and after accounting for the environment was computed using the entire PCA and the residuals of the entire RDA, respectively (Lebreton *et al.*, 1991). Additionally, we also computed SAC for the first and second PCA axes. All Moran's I values were tested using Monte Carlo permutations (999 runs). Finally, Moran's I values before and after accounting for environmental variables were compared to the dispersal values of the taxonomic groups. All statistical analyses and graphical outputs were computed with the R freeware (R Development Core Team, 2010) and the *ade4*, *pixmap*, and *spdep* libraries.

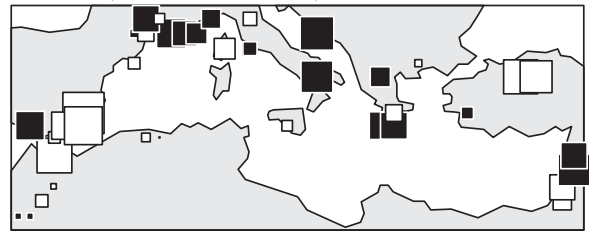
RESULTS

Exogenous and endogenous factors

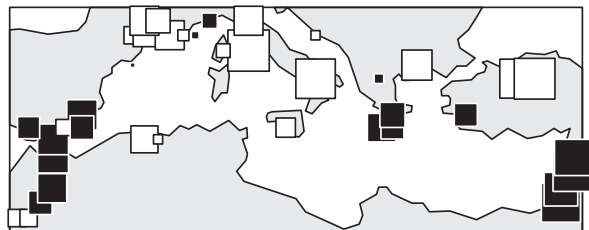
The two climatic variables had significant Moran's I values (Fig. 2). Overall, rainfall was higher in northern Mediterranean spatial units, whereas temperature was lower there. Concerning other site characteristics, elevation also had a significant Moran's I , whereas river size and water hardness did not have such significance. High elevation sites were mainly located in North Africa, Corsica and central Greece. Most streams had a small size (i.e. < 10 m) but varied in water hardness.

Mean affinity values for aerial dispersal were high for Odonata and Coleoptera, whereas the highest values of aquatic dispersal were found for Crustacea and Mollusca (Table 1). Genera with aerial passive dispersal occurred only among the Trichoptera, Ephemeroptera, Heteroptera and Mollusca. All

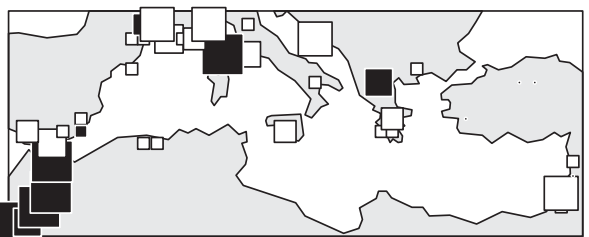
Rainfall (Moran's $I = 0.265^*$)



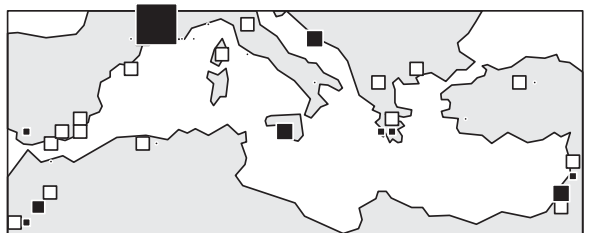
Temperature (Moran's $I = 0.488^{**}$)



Elevation (Moran's $I = 0.327^*$)



River size (Moran's $I = -0.086$)



Water hardness (Moran's $I = -0.021$)

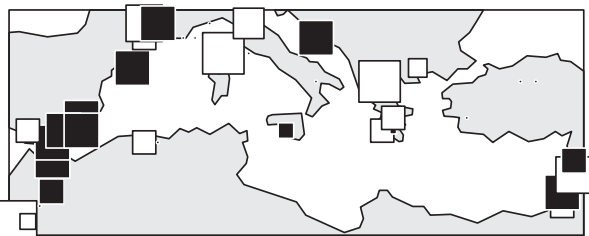


Figure 2 Plot of centred values (i.e. the value of each spatial unit minus the average of all spatial units), indicated by the size of squares, of the five selected environmental variables in the 39 spatial units shown in Fig. 1. Black squares correspond to spatial units with values of the environmental variables higher than the mean whereas white squares indicate the contrary. Values of Moran's I and their significance using Monte Carlo permutations (999 runs) are also shown (* for $P < 0.05$ and ** for $P < 0.01$).

taxonomic groups had genera with aquatic passive and active dispersal. As a result, the overall dispersal index was high for Odonata and Coleoptera, intermediate for Trichoptera,

Table 1 Number of genera, mean affinity values for each dispersal category (in %) derived from Tachet *et al.* (2002), and overall dispersal index and standard deviation for each taxonomic group of stream invertebrates studied (see Materials and Methods for details). Taxonomic groups are arranged by decreasing dispersal index.

	Number of genera	%Aquatic passive	%Aquatic active	%Aerial passive	%Aerial active	Dispersal index	Standard deviation
Odonata	22	21.5	16.6	0	61.9	13.43	2.31
Coleoptera	58	16.8	22.6	0	60.6	13.42	2.80
Trichoptera	61	23.0	23.5	19.9	33.6	10.11	2.05
Ephemeroptera	25	28.1	21.8	15.7	34.4	9.82	1.33
Heteroptera	19	16.7	44.1	5.2	34.0	9.69	3.26
Plecoptera	23	34.6	42.1	0	23.3	7.12	0.98
Crustacea	10	40.7	59.3	0	0	3.37	1.64
Mollusca	30	61.8	31.0	7.2	0	2.88	0.95

Ephemeroptera, Heteroptera and Plecoptera, and low for Crustacea and Mollusca.

Taxonomic richness and composition

Genus richness differed across streams of the Mediterranean Basin, and some general patterns were observed for some insect groups (Fig. 3). Genus richness of Heteroptera and Coleoptera was high in the streams of the western Mediterranean Basin, whereas that of Ephemeroptera, Plecoptera and Trichoptera was relatively high in the streams of the northern side. Odonata had patchy richness, although their richness was

higher in the southern Iberian and Greek streams. Non-insect groups had less consistent spatial richness patterns, but streams of the middle-east region had relatively higher richness of Crustacea and Mollusca. Only Trichoptera, Heteroptera and Plecoptera showed significant SAC for richness. With the exception of Odonata richness, our selection of environmental variables significantly contributed to explaining the variability of richness in the other taxonomic groups (Table 2). Temperature was a significant variable for Trichoptera, Ephemeroptera and Plecoptera, with higher richness of these orders found at lower temperature. Coleoptera and Heteroptera richness were negatively related to river size and positively to water hardness,

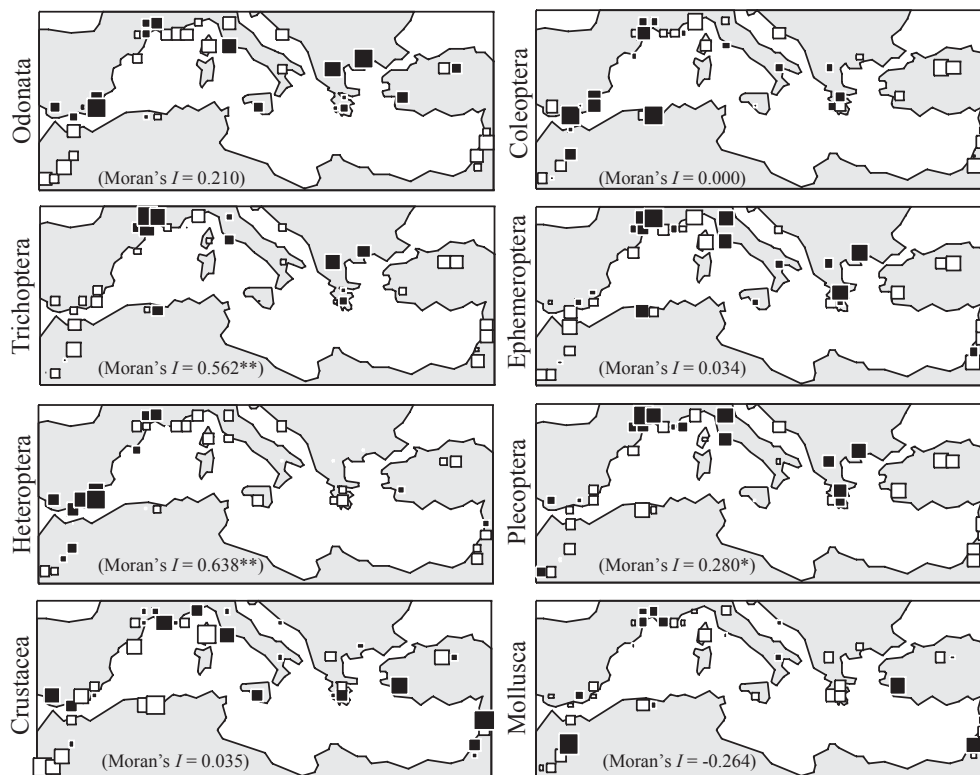


Figure 3 Plot of centred genus richness for each taxonomic group of stream invertebrates studied. Taxonomic groups are arranged by decreasing dispersal index (see Table 1) from left to right and top to bottom. See Fig. 2 for further details.

Table 2 Coefficients of five exogenous factors describing genus richness for each taxonomic group of stream invertebrates studied using generalized linear models. Taxonomic groups are arranged by decreasing dispersal index.

	Rainfall	Temperature	Elevation	River size	Water hardness	AIC _c	F	Pr(> F)
Odonata	–	–	–	–	–	–	n.s.	n.s.
Coleoptera	–	–	–	–0.205	0.007	196.86	3.464	0.043
Trichoptera	–	–0.492	–	–	–	207.96	4.928	0.033
Ephemeroptera	–	–0.337	–	–	–	165.93	6.801	0.014
Heteroptera	–	–	–	–0.066	0.003	74.535	10.612	0.000
Plecoptera	–	–0.227	–	–	–0.004	160.44	4.712	0.016
Crustacea	–	–	–0.0006	–	–	49.059	13.32	0.000
Mollusca	–	–	–	–	0.005	162.11	5.710	0.022

AIC_c, second-order AIC; F, F-test value; Pr(> F), probability associated with the F-test.

but the model for Coleoptera was not strongly supported. Mollusca richness increased with water hardness, whereas Crustacea richness decreased with elevation.

Similar to the findings of the richness analysis, the taxonomic composition revealed large spatial patterns for some taxonomic groups (Fig. 4). SAC values on the two-first PCA axes indicated that no large spatial patterns were observed for the first PCA axis of Odonata and Mollusca and for the second PCA axis for most taxonomic groups (Fig. 4). For Coleoptera, Trichoptera, Ephemeroptera and Plecoptera, the first PCA axis indicated some north–south differences, whereas for Heteroptera and Crustacea, differences in the taxonomic composition revealed a mixture of north–south and east–west along the first axis (Fig. 4). Overall, however, only the taxonomic composition of Coleoptera, Trichoptera, Heteroptera and Mollusca was significantly related to the measured environmental variables (Table 3). Considering the first two axes of an RDA, Coleoptera composition was mainly influenced by water hardness, elevation and river size, whereas Heteroptera composition was mainly influenced by river size, water hardness and elevation. Temperature mainly influenced Trichoptera composition, whereas rainfall, temperature and water hardness were the main factors for explaining Mollusca composition.

For genus richness, the significant values of Moran's *I* found for Plecoptera, Heteroptera and Trichoptera, before accounting for the environment, decreased after accounting for the environment. Despite the decrease, the Moran's *I* for the aforementioned groups remained significant (Fig. 5a,b). Similarly, Moran's *I* of the taxonomic composition decreased after accounting for the environment (Fig. 5c,d). Initially, Moran's *I* was significant for all taxonomic groups except for Odonata. After accounting for the environment, Mollusca and Heteroptera no longer had significant Moran's *I*, whereas these values remained significant in the other taxonomic groups (Fig. 5d).

No relationship was observed between Moran's *I* for richness and dispersal index (Fig. 5a,b). In contrast, for taxonomic composition, significant Moran's *I* values decreased with increasing dispersal index after accounting for the environment ($R^2 = 0.883$, $P = 0.017$; Fig. 5d), but this relationship was not significant before accounting for the environment ($R^2 = 0.1878$, $P = 0.6828$; Fig. 5c).

DISCUSSION

As pointed out by others (Lennon, 2000), we found that climatic variables had significant spatial autocorrelation (SAC) in the Mediterranean Basin. However, SAC values were lower for rainfall than for temperature. **Rainfall is usually more variable across space than temperature because it is more influenced by landscape morphology, among other factors (Strahler & Strahler, 1987).** These climatic factors and elevation, the latter also having SAC in our study, have been considered to be relevant in explaining large spatial variability of stream invertebrate richness and composition (Jacobsen *et al.*, 1997; Beauchard *et al.*, 2003; Vinson & Hawkins, 2003).

For genus richness, most of the taxonomic groups that we analysed did not show significant SAC, suggesting that no main large-scale exogenous or endogenous factors were important and that local-scale factors were probably controlling genus richness in each spatial unit (e.g. the absence of leaf litter that restricts the presence of some taxa). However, richness of Plecoptera, Trichoptera and Heteroptera had significant SAC before accounting for the environment. As such, their latitudinal and longitudinal patterns can be related to some measured exogenous factors, such as temperature and elevation (Plecoptera and many Trichoptera genera have low temperature and higher elevation preferences; Haidekker & Hering, 2008) or water hardness (Heteroptera richness depends on water acidity; Eyre & Foster, 1989). After accounting for the environment, these three taxonomic groups still had significant SAC, indicating that other non-measured factors (exogenous and endogenous) were also relevant. **For example, surrogates of land use (i.e. a factor not considered here) helped to understand patterns of Trichoptera and Heteroptera in some European regions (Wiberg-Larsen *et al.*, 2000; Karaouzas & Gritzalis, 2006).**

For taxonomic composition, all taxonomic groups except Odonata had significant SAC before accounting for the environment and also showed latitudinal and longitudinal patterns that were influenced by measured exogenous factors. After accounting for the environment, most taxonomic groups had a significant SAC that decreased with their increasing dispersal ability, thereby supporting our hypothesis. The clearest exception from this pattern was observed in the

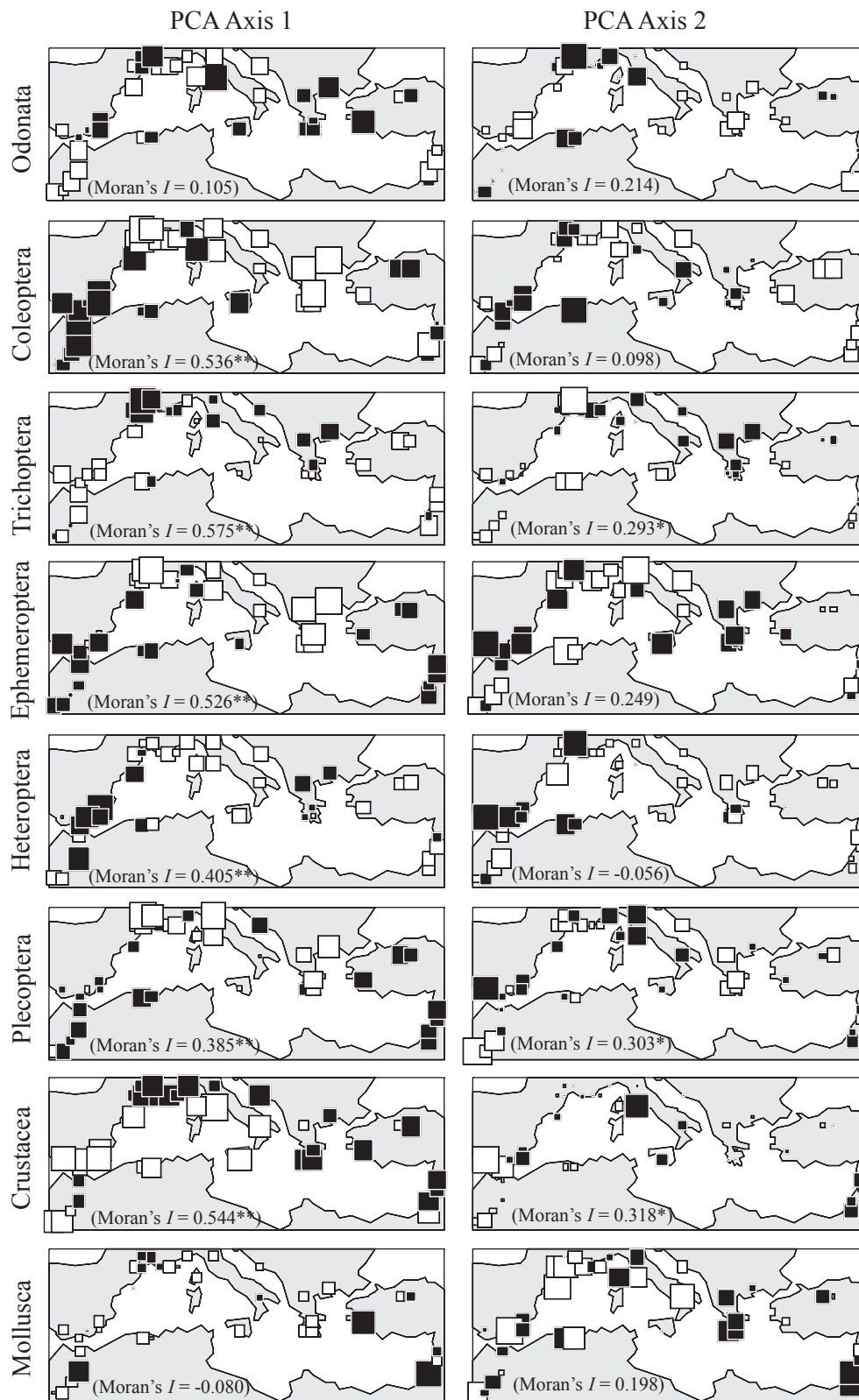


Figure 4 First and second principal components analysis (PCA) axis scores for genus composition of each taxonomic group of stream invertebrates studied. Black and white squares indicate positive and negative values, respectively, on axis 1 and 2; the size of the squares indicates the distance from the intercept along the axis. See Figs 2 & 3 for further details.

Table 3 Coefficients of the redundancy analyses (RDA) performed on each taxonomic group of stream invertebrates in the 39 spatial units (highest values are in bold). Overall explained variability by exogenous factors (Overall R^2) was tested using a permutation test ($n = 999$) on rows of the presence–absence matrix. Taxonomic groups are arranged by decreasing dispersal index.

	RDA axis	Rainfall	Temperature	Elevation	River size	Water hardness	Overall R^2	Simulated- P
Odonata	1	−0.43	0.06	−0.44	−0.20	−0.17	0.129	0.549
	2	−0.07	0.34	0.17	−0.04	−0.17		
Coleoptera	1	0.44	−0.50	−0.77	0.27	0.87	0.197	0.006
	2	−0.34	−0.39	0.17	0.64	0.10		
Trichoptera	1	0.15	−0.79	−0.48	0.26	−0.40	0.183	0.013
	2	−0.27	0.11	−0.47	0.45	−0.45		
Ephemeroptera	1	0.36	−0.74	−0.15	0.02	−0.32	0.169	0.060
	2	−0.18	−0.32	0.07	0.59	0.35		
Heteroptera	1	−0.16	−0.20	−0.21	0.77	−0.72	0.287	0.001
	2	−0.30	0.10	−0.50	−0.05	−0.19		
Plecoptera	1	−0.08	0.60	0.31	0.23	0.50	0.159	0.174
	2	−0.00	0.09	0.44	0.28	−0.33		
Crustacea	1	−0.36	−0.27	0.25	−0.15	−0.01	0.164	0.163
	2	0.30	−0.29	0.17	−0.12	0.21		
Mollusca	1	0.78	−0.68	0.30	−0.37	0.77	0.204	0.016
	2	0.05	−0.17	−0.13	0.30	−0.64		

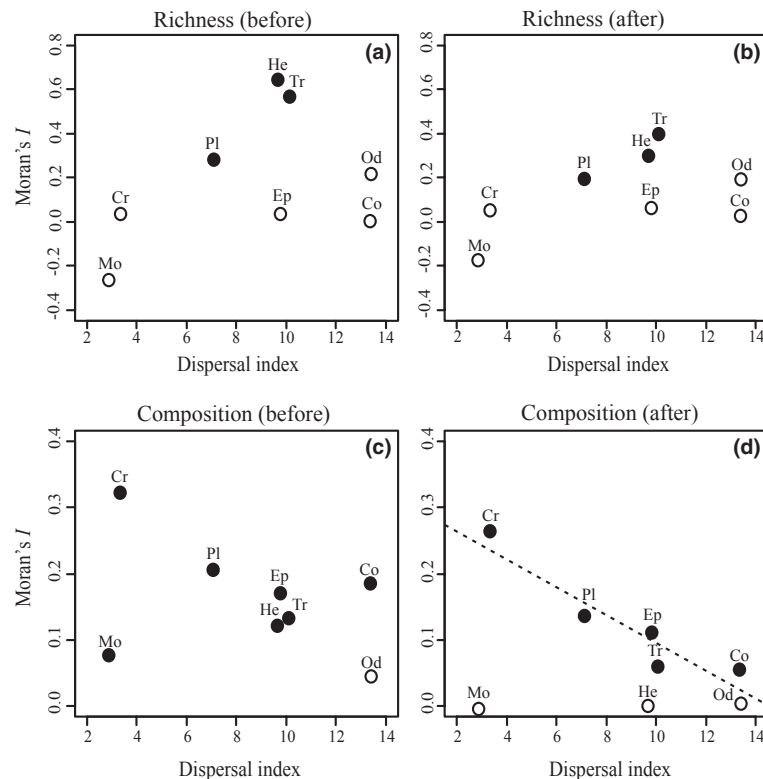


Figure 5 Relationship between Moran's I and dispersal index for (a, b) genus richness and (c, d) genus composition of stream invertebrates, before and after accounting for the environmental variables. Black circles indicate significant spatial autocorrelation (SAC) values at $P < 0.05$ using Monte Carlo permutations (999 runs), whereas white circles indicate non-significant values. The dashed line in (d) shows the linear model using only significant SAC values. Mo, Mollusca; Cr, Crustacea; Pl, Plecoptera; Ep, Ephemeroptera; Tr, Trichoptera; He, Heteroptera; Od, Odonata; Co, Coleoptera.

Odonata, which did not have significant SAC. There is evidence that some Odonata are able to migrate across continents and are strong generalists (Bohonak & Jenkins, 2003; Schindler *et al.*, 2003; Wikelski *et al.*, 2006). This evidence indicates that they can reach all sites and inhabit most of them, which explains the very low and non-significant SAC found for this group even before accounting for the environment. Contrary to our hypothesis, Mollusca had a very low SAC, which was explained by measured environmental variables (i.e. SAC was not significant after accounting for the environment). Therefore, one potential explanation is that consistent large spatial patterns of this group can be precluded by its low dispersal ability; in addition, members of this group are very sensitive to local environmental factors (e.g. macrophyte diversity, Brönmark, 1985), resulting in narrow distribution ranges (Ponder & Colgan, 2002).

Beyond the dispersal potential, however, other factors can also explain SAC of richness and composition after accounting for environmental effects. Other large-scale environmental variables not available in the dataset could have been relevant for invertebrates (van Teeffelen & Ovaskainen, 2007), such as historical factors (Lobo & Davis, 1999; Beauchard *et al.*, 2003), land use (Sandin & Johnson, 2004) or other climatic variables (e.g. number of rainy days; Beauchard *et al.*, 2003). However, the taxonomic resolution used in our study (i.e. genus level) is coarse enough to rule out historical factors in the studied region, and we used current environmental variables that directly or indirectly relate to already known patterns of stream invertebrates. Thus, for example, precipitation has been used as a surrogate of hydrological disturbance (Vinson & Hawkins, 2003) or elevation and river size may also be surrogates of available energy for stream invertebrates (e.g. leaf litter; Vannote *et al.*, 1980; Minshall *et al.*, 1985). Our analysis did not include exogenous local-scale factors (e.g. presence of macrophytes), but these would rarely show SAC at large-scale unless correlated to large-scale factors. Endogenous factors other than dispersal (e.g. feeding strategies) may also be related to SAC; however, at the spatial scale considered by us, dispersal is viewed as very important for stream invertebrates (Bohonak & Jenkins, 2003). Likewise, for terrestrial invertebrates, Cleary *et al.* (2009) suggested that dispersal explains large-scale geographic patterns and found that other endogenous factors, such as feeding strategies, were more strongly associated with local habitats (e.g. logged versus unlogged forest). Therefore, our large-scale analysis demonstrates that, except for Mollusca, the composition of taxonomic groups with low dispersal potential shows high SAC after accounting for exogenous factors, whereas high-dispersal organisms have low or non-significant SAC. Thus, our results provide an empirical demonstration that dispersal, together with exogenous factors, is strongly influencing spatial patterns of the taxonomic composition of organisms but not of their richness.

The relative importance of exogenous and endogenous factors for species distributions is currently a controversial issue in community ecology. Ecologists have commonly considered exogenous factors and niche-based models to

explain assemblages; however, more recent views derived from neutral models give much more weight to endogenous factors (i.e. dispersal; Hubbell, 2001). Attempts to test neutral models with stream invertebrates reported that both exogenous and endogenous factors are affecting spatial patterns of these organisms (Thompson & Townsend, 2006), which corresponds to views prevailing *c.* 100 years ago (e.g. Thienemann, 1918). Our results support these old and recent ideas, but they indicate that the relative importance of both factor types varies between taxa, with both types being particularly important for taxa with intermediate levels of dispersal. Therefore, our results overall supported our hypotheses, so we conclude that exogenous and endogenous factors have to be addressed in combination in large-scale studies, because ignoring one of them can lead to misunderstandings of community patterns.

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BIOSKETCHES

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