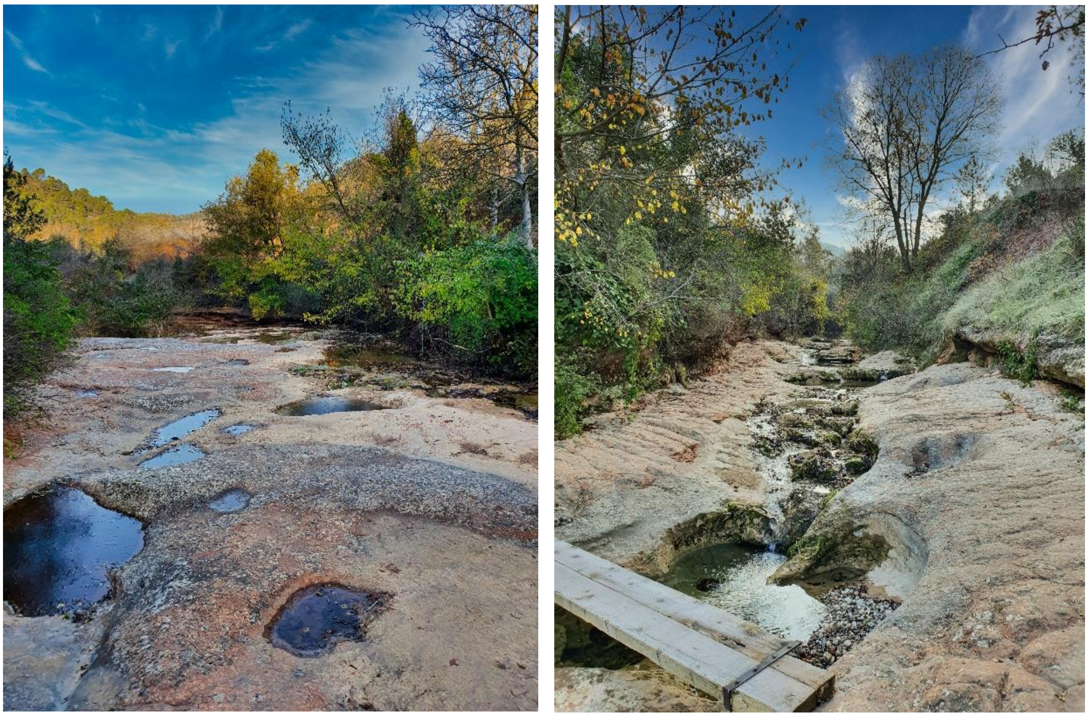
Master's degree in Ecology, Environmental Management and Restoration

BACK TO THE FUTURE: MACROINVERTEBRATE COMMUNITIES RECOVERY IN INTERMITTENT RIVERS AFTER THE DRY SEASON



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ABSTRACT

Intermittent rivers and ephemeral streams (IRES) are the most common fluvial ecosystems in the world. They will become even more abundant in the future due to climate change and increased water abstraction. IRES are rivers that cease to flow (seasonally or sporadically) at some point(s) along their course. Despite the importance of IRES and their unique biodiversity, there are important aspects of their ecology and management that remain poorly understood. For example, few studies have investigated the rewetting period, i.e., the moment of flow resumption that occurs after the dry period. Here, we tested the response of taxonomic and functional features along hydrological and spatial isolation gradients across eight IRES in a Mediterranean region during the rewetting. We found a strong influence of hydrological isolation (i.e., low flow permanence) and a lower (yet significant) effect of spatial isolation on the macroinvertebrate communities. Those sites with lower hydrological and spatial isolation showed higher taxonomic richness (also EPT and OCH richness), functional richness, functional redundancy and functional dispersion. In contrast, we found poor communities dominated by Chironomidae and other Diptera with high mean functional similarity in the most intermittent and ephemeral sites. Moreover, the results of spatial isolation and dispersal traits analyses suggested that the recolonisation of macroinvertebrates to the rewetted sites was mainly produced through the river network, especially through long-distance dispersal events by drift favoured by preceding flash floods. The amount of water bodies located at one kilometre around the sites (i.e., surrounding water bodies) did not show any significant correlation with any of the community metrics, suggesting that aerial recolonisation through overland dispersal from nearby refugia was not important.

RESUM

Els rius intermitents i les rieres efímers (IRES) són els ecosistemes fluvials més comuns del món. En el futur seran encara més abundants a causa del canvi climàtic i l’augment de captació d’aigua. Els IRES són aquells rius que deixen de fluir (estacionalment o esporàdicament) en alguns punt(s) al llarg del seu curs. Malgrat la importància dels IRES i la seva singular biodiversitat, hi ha aspectes importants de la seva ecologia i gestió que encara queden per resoldre. Per exemple, pocs estudis han investigat el període de “rewetting”, és a dir, el moment en què es produeix la represa del flux d’aigua després del període sec. Aquí, es va provar la resposta de característiques taxonòmiques i funcionals al llarg de gradients d’aïllament hidrològic i espacial a través de vuit IRES a una regió mediterrània durant el “rewetting”. Es va trobar una forta influència de l'aïllament hidrològic (és a dir, baixa permanència del flux) i un menor (però significatiu) efecte de l'aïllament espacial sobre les comunitats de macroinvertebrats. Aquelles localitats amb menor aïllament hidrològic i espacial van mostrar una major riquesa taxonòmica (també la riquesa d’EPT i OCH), i riquesa, redundància i dispersió funcionals. En canvi, es van trobar comunitats pobres dominades per Chironomidae i altres Diptera amb una semblança funcional mitjana alta entre tàxons a les localitats més intermitents i efímeres. A més, els resultats de l’anàlisi de l’aïllament espacial i dels trets de dispersió van suggerir que la recolonització dels macroinvertebrats durant aquest moment es produïa principalment a través de la xarxa fluvial, sobretot a través d’esdeveniments de dispersió a llarga distància per deriva afavorida per les grans riuades succeïdes. La quantitat de masses d’aigua situades a un quilòmetre al voltant de cada localitat (és a dir, les masses d’aigua circumdants) no van mostrar cap correlació significativa amb cap de les mètriques de comunitat, cosa que suggereix que la recolonització aèria mitjançant la dispersió terrestre des de refugis propers no va ser important.

CONTENTS

1. INTRODUCTION

Despite being largely ignored in the past, river ecosystems that recurrently cease to flow of dry up at some point in time and space (hereafter Intermittent Rivers and Ephemeral Streams, IRES) constitute more than half of the length of the global river network (Datry *et al.*, 2014a). They are complex mosaics of terrestrial and aquatic habitats that vary greatly through time and across landscapes (Bogan *et al.*, 2017). In the coming decades, the number and length of IRES will increase in many regions due to climate, land-cover changes and increasing water abstraction for irrigation and other economic uses (Palmer *et al.*, 2008, Larned *et al.*, 2010).

IRES are especially common in Mediterranean climates (Cid *et al.*, 2017). In these regions, stream ecosystems are hydrologically diverse and highly dynamic shifting-habitat mosaics (Bonada & Resh, 2013; Acuña *et al.*, 2015). They are subjected to seasonal and predictable natural disturbances, such as floods and droughts (McElravy *et al.*, 1989; Gasith & Resh, 1999), which are considered to be evolutionary pressures that constrain plant and animal communities (di Castri, 1981; Stamou, 1998). At the temporal scale, intra- (i.e., seasonal) and inter-annual variability in precipitation and temperature influences flow dynamics. At the spatial scale, spatial variability in precipitation and temperature patterns combined with topographic variation lead to spatial variation in hydrologic patterns and habitat connectivity (Cid *et al.*, 2017; Sarremejane *et al.*, 2017b).

Three stream types can be distinguished in Mediterranean streams: perennial (flowing waters), intermittent (mostly isolated pools during the dry season that may persist to the end of summer) and ephemeral (dry stream beds in the dry season or even for longer periods) (Bonada *et al.*, 2007). These stream types comprise a gradient of hydrological isolation (i.e., the different duration of no-flow or no surface water), from null isolation in perennial streams, seasonal isolation in intermittent streams, and prolonged (i.e., inter-annual) isolation in highly ephemeral streams. In intermittent streams, seasonal hydrological variability can be divided into four different periods: 1) a period of hydrological *stress relief* during winter and spring with connected riffles and pools; 2) a drying period with isolated pools between late spring and early summer; 3) a dry period with dry riverbeds between mid-summer and early autumn; and 4) a rewetting period in early autumn (Hershkovitz & Gasith, 2013; Sarremejane *et al.*, 2017b) (Fig. 1).

Between late spring and early summer, the loss of riffles, the increase of water temperature and the decrease of oxygen concentrations eliminate many lotic taxa, such as EPT (Ephemeroptera, Plecoptera and Trichoptera) (Boulton & Lake, 2008). With increasing drying, pools decrease in size and the densities of organisms can increase dramatically, leading to strong intra- and interspecific interactions, such as competition or predation (Datry *et al.*, 2016). At this moment, pool conditions are uninhabitable by many stream insects, so lentic taxa as OCH (Odonata, Coleoptera and Hemiptera) and certain Diptera, such as Chironomidae, increase their relative abundances (e.g., Acuña *et al.*, 2005; Bogan & Boersma, 2012, Bonada *et al.*, 2012). These pools may dry-out completely although flow may continue through hyporheic sediments below the streambed (Costigan *et al.*, 2017). If drying continues, hyporheic flows may also cease. Mediterranean river species have several morphological (e.g., small size, soft body) and physiological (e.g., crawling, borrowing) adaptations that can withstand these conditions, activating resistance strategies to desiccation (Hershkovitz & Gasith, 2013), exploiting on-site refugia (Chester & Robson, 2011) or sheltering in the hyporheic zone (del Rosario & Resh, 2000) or in the dry riverbed (Verberk *et al.*, 2008) (Fig. 1).

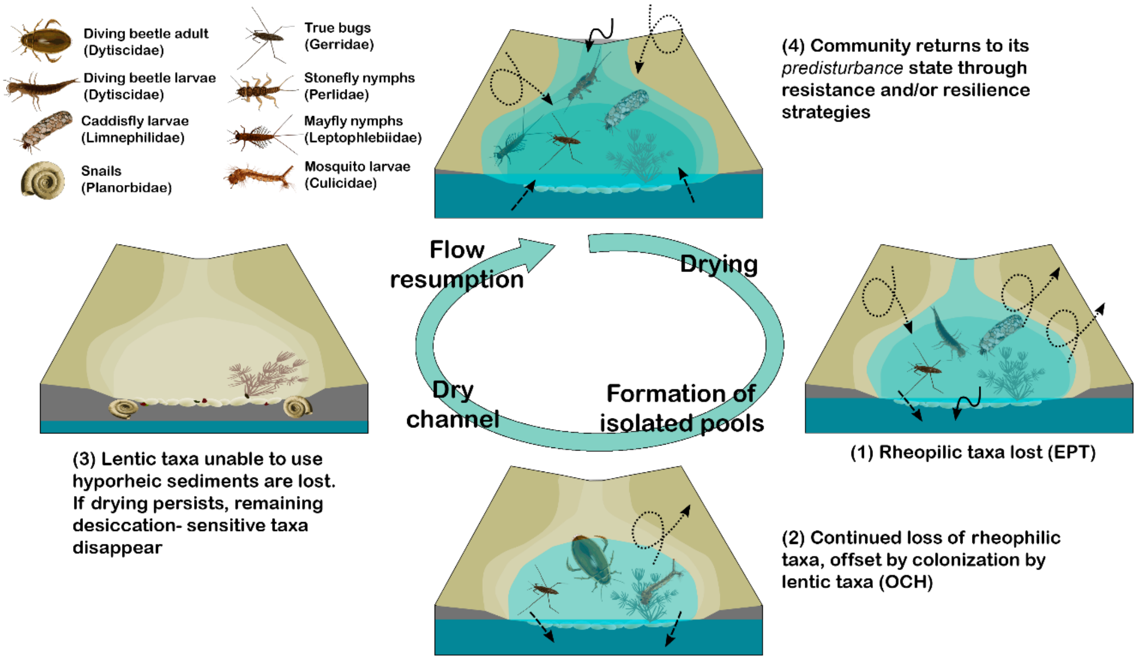

Figure 1. Transition between flowing, isolated pools and drying phases in Mediterranean intermittent streams along the different seasons of the year. Flow cessation begins in late spring and flow resumption starts in early autumn. Macroinvertebrate groups represented: Ephemeroptera (Leptophlebiidae), Plecoptera (Perlidae), Trichoptera (Limnephilidae), Coleoptera (Dytiscidae), Hemiptera (Gerridae), Diptera (Culicidae) and Gastropoda (Planorbidae). Drawings: Pau Fortuño Estrada. Not to scale.

In early autumn, localised precipitation can lead to rewetting (i.e., flow resumption, Fig. 1) and dry riverbeds shifting to a series of riffles connected to pools (Datry *et al.*, 2014a). Rewetting usually coincides with the onset of the first autumn rainfalls although in some

IRES, there may be several “false starts” if rainfalls are not important (Boulton *et al.*, 2017). Nevertheless, rewetting in Mediterranean rivers is usually triggered by increased precipitation and runoff in the headwaters, sometimes intense enough to cause flash floods that increase connectivity among habitat patches (Thomaz *et al.*, 2007) and swiftly transform channels from completely dry to flowing strongly (Jacobson *et al.*, 2000; Cohen & Laronne, 2005). Community recovery upon rewetting is gradual over time and the temporal dynamics of drying events (including their frequency and duration) induce a wide range of recovery patterns (Larned *et al.*, 2010). Species richness generally increases through time, with some species returning quickly and others colonising later, depending on its life-cycle duration and synchronisation with flow resumption (Bogan *et al.*, 2017).

In river networks, the unidirectional flow of water drives organism longitudinal dispersal and material transport from upstream to downstream (Brown & Swan, 2010). However, dispersal of organisms also occurs in lateral, vertical and temporal dimensions (Fullerton *et al.*, 2010), via water or air. In water, organisms crawl or swim actively, or drift passively (Bilton *et al.*, 2001), depending on the presence and amount of water, as well as slope and other geomorphological characteristics (Datry *et al.*, 2017). Aerial dispersal occurs actively by flying stages of insects or passively by wind or biotic vectors (Bilton *et al.*, 2001). The different proportions of these dispersal events shape the different processes of colonisation of the new rewetted habitats and, therefore, the recovery time after drying. These processes include: (1) resistant strategies; colonisation of surface habitats from the hyporheic zone through the emergence of desiccation-resistant forms (temporal dispersal; Bonada *et al.*, 2017) or through species that have survived in the isolated pools, and 2) resilient strategies; recolonisation via dispersal of organisms from perennial refuges via water or air (spatial dispersal; Datry *et al.*, 2014b, Bonada *et al.*, 2017) (Fig. 1). The first strategy was examined by previous authors assessing the potential of dry streambed sediments as a refuge by rewetting dry sediment samples under controlled conditions (e.g., Storey & Quinn, 2013). However, its efficiency in such contribution is variable and not completely understood (Stubbington & Datry, 2013). In fact, temporal dispersal does not seem relevant for macroinvertebrate community recovery in our study area according to a recently performed sediment rewetting experiment (Folch, 2020). In this experiment, no macroinvertebrates emerged from the dry sediment after its rehydratation, suggesting the lack of drought-resistance strategies. Conversely, resilience via spatial dispersal is frequently cited as the most important community recovery strategy in IRES (Acuña *et al.*, 2005; Chester & Robson, 2011) and the ability to disperse between and within streams (via overland flight, crawling, drift dispersal and swimming) is widely documented among IRES taxa (e.g., Williams & Hynes, 1976; Lake, 2011).

One important factor which represents a high constraint on recolonisation due to dispersal limitation in headwater intermittent sites is spatial isolation. The position of a given site within the stream network (e.g., its geographical proximity to perennial refuges and intermittent reaches) is a primary driver of macroinvertebrate diversity and community composition in IRES, due to its regulatory effect on aerial and aquatic colonisation (Bogan & Boersma, 2012; Bogan *et al.*, 2013; Cañedo-Argüelles *et al.*, 2015). This colonisation rate occurs as a function of distance to perennial refuges, with faster recovery corresponding to shorter distances (Robson *et al.*, 2011). There is a wealth of literature about the use of river network as the main ‘highway’ for dispersal (Petersen *et al.*, 2004), although more recent studies (e.g., Cañedo-Argüelles *et al.*, 2015; Razeng *et al.*, 2016) found that overland pathways, using perennial refuges as stepping-stones, might be the main connections to sources of recolonists in fragmented stream networks (i.e., including dry stream reaches at some point in time).

Numerous researchers examined macroinvertebrate communities in perennial rivers vs IRES, or in isolated pools vs flowing reaches of IRES (e.g., Acuña *et al.*, 2005; Bonada *et al.*, 2007). However, more recent studies (e.g., Schriever *et al.*, 2015; Datry *et al.*, 2014b; Crabot *et al.*, 2020) assessed flow permanence as a continuous variable (e.g., the frequency and duration of zero-flow periods before flow resumption) showing spatial and temporal gradients (Larned *et al.*, 2011). Most studies have focused on taxonomic metrics (e.g., taxa richness and abundance). However, these metrics typically provide limited insight into the impacts of disturbance on ecosystem functioning (Mouillot *et al.*, 2013). In contrast, trait-based indices of community structure can be more informative in describing ecological responses to environmental variability (Walker, 1992; Cadotte *et al.*, 2011). For example, Bonada *et al.* (2007) found no difference in macroinvertebrate species richness between perennial and intermittent rivers but did find significant among-site trait differences attributable to hydrology. Community functional diversity measures such as functional richness and functional redundancy are often used and correlated positively, where loss of species produced by natural stressors (e.g., hydrological isolation) results in loss of functional diversity at the community level (Gutiérrez-Cánovas *et al.*, 2015). Biological traits describe any morphological, physiological, or phenological feature usually measurable at the individual level (Mouillot *et al.*, 2013). Macroinvertebrates exhibit a great diversity of biological traits (Statzner *et al.*, 2004; Poff *et al.*, 2006) since they are present over a wide range of environmental conditions

(Rosenberg & Resh, 1993; Merritt *et al.*, 2008) and possess a wide range of dispersal capacities (Bilton *et al.*, 2001; Sarremejane *et al.*, 2020).

The aim of the study was to characterise the macroinvertebrate communities established during the rewetting period, after a high rainfall event that caused flash floods reconnecting longitudinal flow. We analysed the relative importance of the preceding hydrological conditions (i.e., hydrological isolation or flow permanence) and the effect of spatial isolation on the composition and structure of the macroinvertebrate communities. Considering taxonomic and functional metrics from IRES differing in hydrological and spatial isolation, we tested the following hypotheses:

> **H1**: Macroinvertebrate composition upon rewetting would be significantly determined by antecedent flow duration due to both environmental filtering and spatial isolation (Arscott *et al.*, 2010; Larned *et al.*, 2010; White *et al.*, 2017). In this sense, we expected that the effect of spatial isolation would be less important than hydrological conditions, as the latter was considered previously a major driver of stream macroinvertebrate communities (Datry *et al.*, 2014b; Schriever *et al.*, 2015) and metacommunities (Cañedo-Argüelles *et al*., 2020).
>
> **H2**: Macroinvertebrate communities in perennial and spatially connected streams would be characterised by higher taxonomic richness (Fig. 2a). A previous study showed that taxonomic richness decreased linearly along gradients of flow intermittence in several rivers around the world (Datry *et al.*, 2014b). The most perennial streams offer relatively stable environmental conditions (Sarremejane *et al.*, 2017b) and the less spatial isolation enhances the probability to be more connected with nearby perennial waters that could act as a potential sources of IRES recolonists (Bogan & Boersma, 2012).
>
> **H3**: Flow permanence and EPT richness would be significantly and positively correlated (Fig. 2b) due to a higher presence of riffles favouring lotic species. Conversely, we expected a negative correlation between flow permanence and OCH richness (Fig. 2c) due to less presence of pools. Also, we expected the same negative relationship between flow permanence and % richness of Chironomidae (Fig. 2d) and % richness of non-Chironomidae Diptera taxa (i.e., % richness other Diptera) (Fig. 2e) because these taxa are generalists and ubiquitous, and in terms of relative richness, they would be more important than EPT and OCH in the most intermittent and ephemeral sites (Stubbington *et al.*, 2017).

H4: Functional community structure would significantly change along hydrological and spatial isolation gradients. In particular, at the whole-community level, we expected an increase in functional richness (Fig. 2f), functional dispersion (Fdis) (Fig. 2g) and functional redundancy (FR) (Fig. 2h) with higher flow permanence and spatial connectivity (Schriever *et al*., 2015). Since both, local hydrological conditions and spatial connectivity, should affect community structure, we expected that these functional metrics would respond to combinations of both gradients (Cañedo-Argüelles *et al*., 2020). In IRES, drying can exert strong environmental filtering (species with no drought adaptations are not able to survive), thereby lowering functional richness. Conversely, in perennial streams trait diversification could be promoted due to temporal stability of environmental conditions, allowing for more species and functional traits to coexist through niche partitioning (Villéger *et al.*, 2011). Thus, we expected a higher functional dispersion and functional redundancy in more perennial streams. At the taxon functional level, we predicted that the mean functional similarity between taxa (Fsim) (Fig. 2i) would be highest in temporary and spatially isolated streams, as environmental filtering would be strongest and the chances for colonisation from perennial streams would be lowest (Bogan & Boersma, 2012).

H5: Aquatic passive dispersal (Fig. 2m) would be more important than aerial active dispersal during the rewetting (Fig. 2j), because high stream flows could allow massive passive drift dispersal events of organisms from upstream reaches. Aerial passive (Fig. 2k) and aerial active dispersal would respond identically to both hydrological and spatial isolation gradients, and the same for aquatic active (Fig. 2l) and aquatic passive dispersal. Although aerial dispersal could be possible since all the sites sampled were near each other, some taxa (e.g., Odonata) have relatively long life cycles (+1 year long) and require more time in the water to emerge from eggs deposited by flying adults that recolonise rewetted habitats from perennial refuges (Bogan & Boersma, 2012).

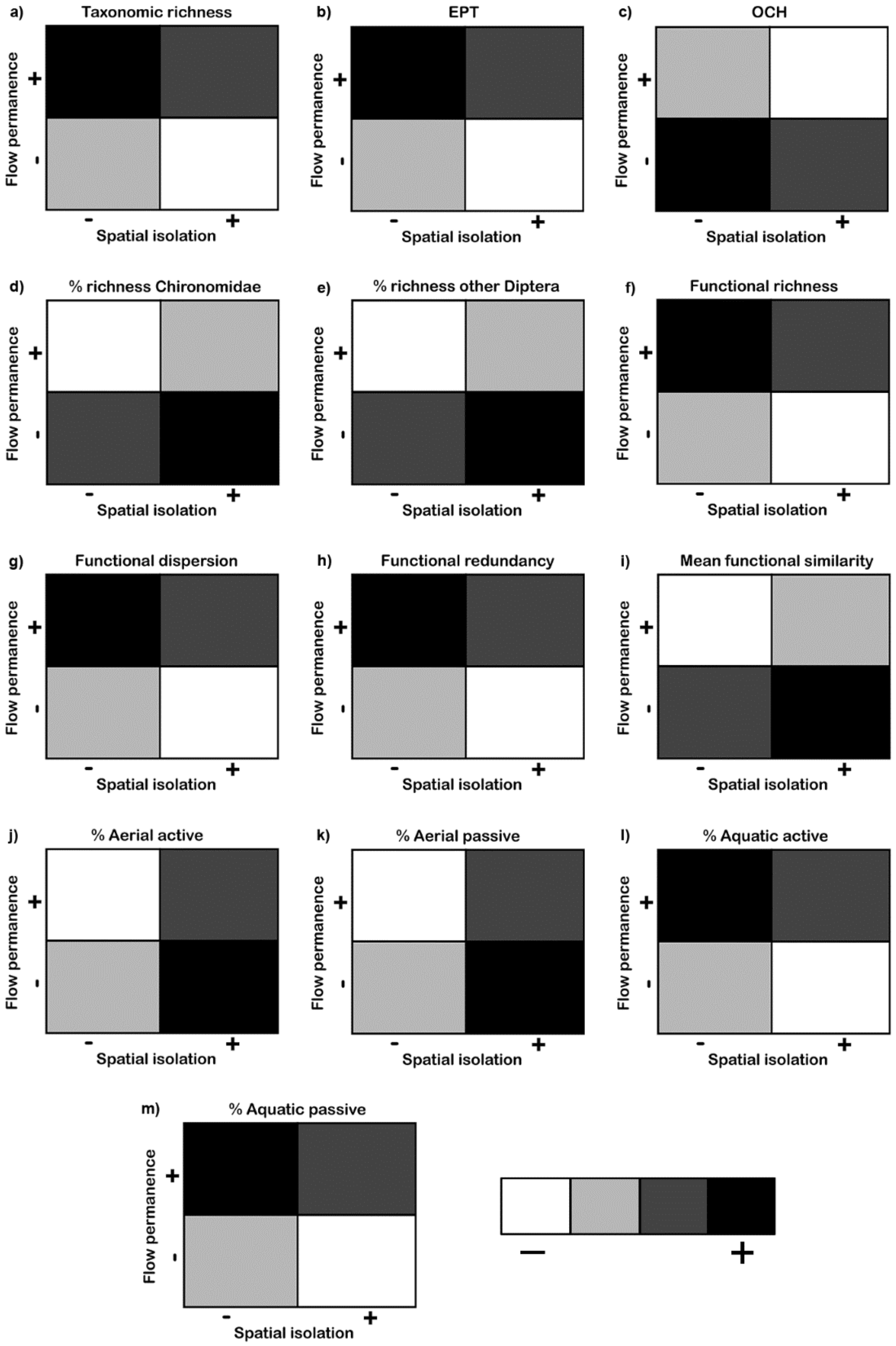

Figure 2. A two by two matrix was used to represent the expected patterns occurring in macroinvertebrate communities of IRES in space (spatial isolation) and time (hydrological isolation, here as low flow permanence). The X-axis corresponds to spatial isolation, which includes both dispersal through the river network and aerial recolonisation from isolated perennial refuges. The Y-axis corresponds to hydrological isolation. Both variables studied were categorised into two levels, low (-) and high (+). Every response variable had 4 different levels represented by grayscale, from black (higher values) to white (lower values). For example, in the upper-left cell, a sampling site would belong to a perennial and low spatially isolated reach, whereas in the lower-right cell to an intermittent spatially isolated reach. Response variables studied: (a) taxonomic richness; (b) EPT richness; (c) OCH richness; (d) % richness of Chironomidae taxa; (e) % richness other Diptera; (f) functional richness; (g) functional dispersion; (h) functional redundancy; (i) mean functional similarity between taxa; (j) % aerial active dispersal; (k) % aerial passive dispersal; (l) % aquatic active dispersal; (m) % aquatic passive dispersal.

2. MATERIAL AND METHODS

2.1. Study area

The study was carried out in Sant Llorenç del Munt i l'Obac Natural Park, a protected area in the Vallès Occidental region (Catalonia, NE Spain) (Fig. 3). The area has a Mediterranean climate, with irregular and heavy rainfalls in the spring and autumn, and a dry climate in summer (Rieradevall *et al.*, 1999). The Park has a dominant karstic geology with highly permeable substrates and, therefore, surface flow in streams may cease in hours or days after rainfall. Almost all streams within the park dry up during summer (either with isolated pools or completely dry riverbeds), and the few that do not dry have very low flows (Rieradevall *et al.*, 1999). Perennial streams in this area are mostly linked to springs that discharge from the karstic aquifer (the most permanent ones are situated at low altitudes) (Bonada *et al.*, 2007). The river network belongs to two main river catchments that discharge into the Mediterranean Sea: the Besòs River and the Llobregat River.

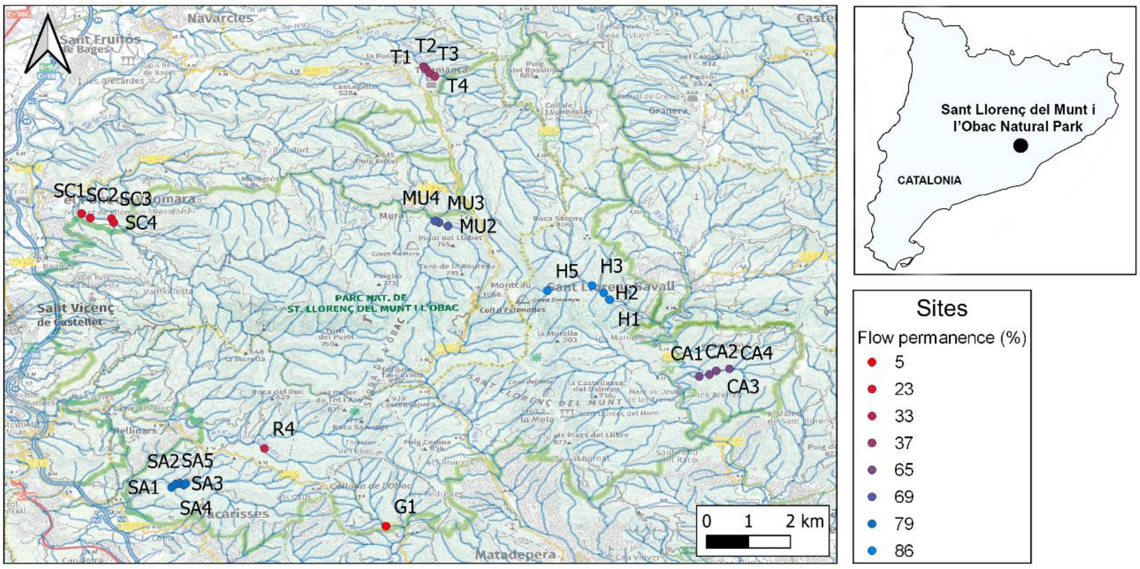

Figure 3. Locations of sampling sites at Sant Llorenç del Munt i l'Obac Natural Park. The thick green line indicates the limits of the Park. Streams sampled: "Rellinars" (R), "Castelló" (CA), "Vall d'Horta" (H), "Mura" (MU), "Gaià" (G), "Sanana" (A), "Talamanca" (T) and "Santa Creu" (SC). Flow permanence (%) is represented for each site and was assessed through temperature data-loggers (Valera, 2020).

2.2. Macroinvertebrate collection and processing

We sampled 8 pristine subcatchments (i.e., streams) comprising reaches that cover a wide range of hydrological conditions, from ephemeral (<24% water permanence) to perennial (100% water permanence) sites (Fig. 3). Samples were collected during the rewetting, from 18th to 21st November 2019. Previously to rewetting, a cold drop affected Catalonia and caused extremely rapid rain episodes and flash floods (Fig. 4; Fig. 5) (e.g., Rellinars automatic station registered 41.7 mm in only 30 minutes on 22nd October 2019; Servei Meteorològic de Catalunya, 2019a). Although these flash floods occurred only one month before the sampling, previous studies reported that macroinvertebrate communities can recover within days to weeks to pre-flood characteristics (e.g., abundance, taxonomic composition) (Mackay, 1992; Matthaei *et al.*, 1997; Robinson *et al.*, 2003a,b).

In each stream, we placed an average of 4-5 sampling sites (Fig. 3), depending on their size and accessibility. Each site consisted of a 100-m-long stream reach and was separated about 100-200 m from its nearest sampling site. Macroinvertebrates were taken with a 250 μm mesh size net, using the kick method trying to cover all microhabitats and having a representation of both riffles and pools. A total amount of 26 samples were collected and preserved in 96% ethanol. At the laboratory, macroinvertebrates were sorted, counted and identified to the lowest practical taxonomic level (mostly genus). Several taxa were kept at the family level (e.g., Diptera) or subfamily level (i.e., Chironomidae) because of difficulties in their identification (small organisms or with complex taxonomy). To describe the communities in each dataset in terms of taxonomic composition, we calculated several metrics: taxonomic richness as the number of taxa per sample, EPT and OCH richness, richness of Chironomidae taxa as a % of total richness and % richness of non-Chironomidae Diptera taxa (i.e., % richness other Diptera).

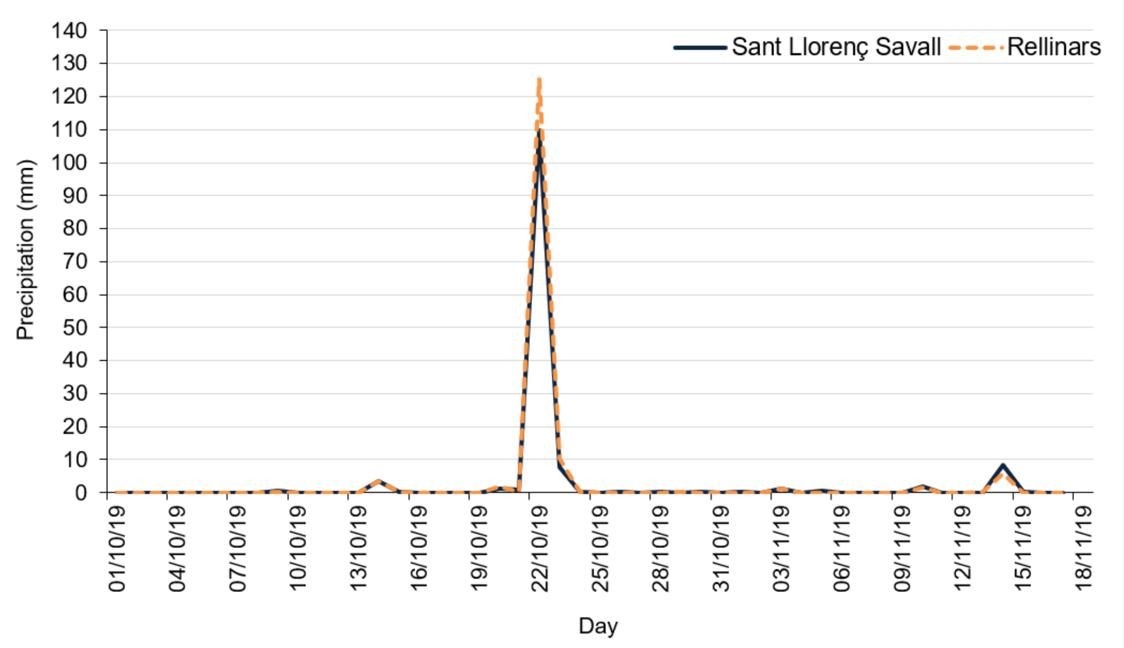

Figure 4. Daily precipitation data (mm) registered at Sant Llorenç Savall automatic station (blue line) and Rellinars automatic station (dashed orange line) from 1st October to 18th November 2019 (when sampling period started). Source: Servei Meteorològic de Catalunya, 2019b.

Figure 5. Pictures of sampling sites between 18th and 21st November 2019 after the flash floods occurred during the cold drop in late October: (a) “Castelló” (CA2); (b) “Vall d'Horta” (H3) and (c) “Mura” (MU2). Photos: José María Fernández-Calero.

2.3. Trait analysis

To characterise the functional properties of macroinvertebrate communities, we used 61 categories of 11 biological traits at the genus level from Tachet *et al.* (2010). 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, feeding habits). In particular, four dispersal categories were included (i.e., aerial active, aerial passive, aquatic active and aquatic passive). Trait information for several taxa (mostly crustaceans, Oligochaeta and Hydrachnidiae) was unavailable and, therefore, these taxa were excluded from trait analyses. Diptera were also excluded due to the paucity of detailed trait information on these species and their complex taxonomy (Pfenninger *et al.*, 2007). Within the database, each genus was coded according to its affinity to each trait category using a fuzzy coding approach (Chevenet *et al.*, 1994). The affinity of each genus to each category was coded from 0, for no affinity, to 3 for the strongest affinity, except for feeding and locomotion categories coded from 0 to 5 (Supplementary Material, Appendix 3). Then, 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.

Based on this trait-by-site array, we estimated four functional measures (Table 1) following the same procedure as Gutiérrez-Cánovas *et al.* (2015) that account for the changes in the functional space at the taxon and the whole-community level. Fsim was calculated at the taxon level, while functional richness, Fdis and FR were quantified at the whole-community level.

Table 1. Glossary of functional terms used in trait analyses.

Term	**Description**
Mean functional similarity between taxa (Fsim)	The mean relative overlap between pairs of taxa in a community (Gutiérrez-Cánovas *et al.*, 2015). It goes from zero, when the occurring taxa are functionally distinct, to one when all the taxa composing the community are functionally identical.
Functional richness	The functional space filled by the variability exhibited by each taxon (Stubbs & Wilson, 2004). Values increase when organisms show highly different trait values.
Functional dispersion (Fdis)	The mean distance of all taxa to the weighted centroid of the community in the trait space (Laliberté & Legendre, 2010). Values increase when there are taxa with traits differing greatly from the mean community values.
Functional redundancy (FR)	Occurred where multiple species fulfil similar functional roles, affording communities insurance against species loss (Ricotta *et al.*, 2016). This variable is zero when there is no overlap between taxon pairs, reaching higher values when there are many functionally similar and diverse taxa.

2.4. Environmental variables and hydrological isolation

We measured streamflow and used a multiparameter probe (YSI Professional Plus Multiparameter Probe) to monitor water temperature, dissolved oxygen, pH, conductivity and suspended solids. Moreover, we used the IHF index ("*Índice de Hábitat Fluvial*") to evaluate the instream habitat heterogeneity considering the substrate inclusion in riffles and sedimentation in pools (B1), the frequency of riffles (B2), the substrate diversity (B3), the flow velocity and depth regime (B4), the shade percentage in the channel (B5), the habitat heterogeneity elements (B6) and the aquatic vegetation coverage (B7) (Pardo *et al.*, 2004). We also measured other habitat descriptors, such as % of canopy cover (CC) and the aquatic state (e.g., eurheic, oligorheic and arheic; Gallart *et al.*, 2012). For more detailed information see Supplementary Material, Appendix 2.

Hydrological isolation (flow permanence) was quantified using temperature data loggers (HOBOs) (Valera, 2020), from which it was possible to infer when a specific site was wet or dry (Jensen *et al.*, 2019). Multiple data loggers were placed along the studied stream reaches (both instream and riparian zone) to assess water presence-absence. Specifically, two data loggers were installed at each sampling site: one in a riffle, to determine the day flow ceased and resumed, and one in a pool, to identify the day that the reach dried completely. Unfortunately, many in-stream and riparian loggers were washed out or buried during previous flood events, so we could only calculate a single flow permanence value for each stream (Fig. 3), through the proportion of zero flow days during a certain data logging time (from July to November 2019).

2.5. Spatial isolation

To assess the importance of spatial isolation on recolonisation during rewetting, we estimated two different metrics through the hydrological connectivity between sites and through the presence of perennial refuges that could serve as sources of recolonists. Firstly, we retrieved a stream network from the Institut Cartogràfic i Geogràfic de Catalunya (2015) and delimited the entire river network of the Sant Llorenç del Munt i l'Obac Natural Park (Fig. 6a), and this was then divided into subcatchments, since not all streams are connected. Secondly, a network was built with all the nodes (confluences between streams) (Fig. 6b) using the *igraph* package (Csardi, 2006) in the R environment.

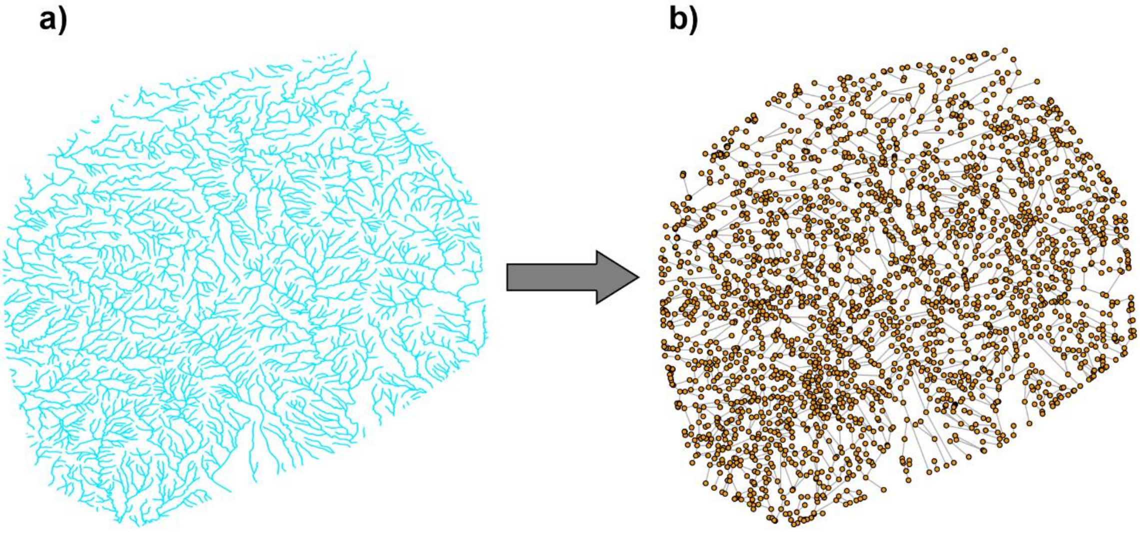

Figure 6. River network of the Sant Llorenç del Munt i l'Obac Natural Park (a) and the same represented as a geometric network (b) with all the confluences between streams (nodes).

Then, we calculated nodes centrality, which is a property of a position in a network and indicates how powerful the position is in terms of connecting the nodes of the network. This centrality can be categorised in different ways. We chose the property of node efficiency which includes a metric called *closeness*. As a network concept, it is a measure of how close on average a node is to every other node in the network. In other words, how many steps are required to access every other vertex from a given vertex. The greater closeness value of a node the lower spatial isolation and the greater connectivity with the rest of the nodes of the river network. Finally, we assigned each sampling site to its nearest node using the *nn2* function in the *RANN* R package (Arya *et al.*, 2019).

We also calculated another spatial metric called *surrounding water*, which represents the total amount of water bodies around each sampling site in a buffer distance of one kilometre, using the *st_buffer* function in *sf* R package (Pebesma, 2018). We chose this buffer distance since previous research suggested that most macroinvertebrate species could colonise from within 5 km (Sundermann *et al.*, 2011), but particularly within the first km of the river network (Tonkin *et al.*, 2014). We associated higher surrounding water values with lower spatial isolation since it increases the chances of macroinvertebrate colonisation from nearby habitats. However, closeness and surrounding water have not the same interpretation. Closeness is calculated including all subcatchments and considering exclusively the dispersion through the river network. Therefore, closeness could be especially important for organisms that use the river network as a dispersal route (e.g., those organisms that are preferentially dispersed by drift). Instead, surrounding water considers any water body within a kilometre, thereby potentially including water bodies that are not connected to the stream network. Thus, surrounding water could be more important for those organisms who disperse by flying and can fly long distances (e.g., Odonata).

2.6. Statistical analyses

We conducted all the analyses in R version 3.5.0 (R Core Team, 2015). We used different R functions in the R packages *vegan* (Oksanen *et al.*, 2019) and *ade4* (Dray & Dufour, 2007) to estimate the four functional measures following Gutiérrez-Cánovas *et al.* (2015). The relationship between taxonomic and functional metrics with hydrological and spatial isolation metrics was tested using generalized linear models (GLMs), assuming a Gaussian distribution of the dependent variables. Closeness was log-transformed to improve linearity with the dependent variables. Moreover, prior to statistical analyses, we explored the correlation between explanatory variables using Spearman's correlation in the *corrplot* package (Wei & Simko, 2017). Also, we tested the correlation between flow permanence, each section of the IHF index and canopy cover, with the aim of better characterising the local environment and finding some possible causes to responses of macroinvertebrate communities.

We used the *mvabund* package (Wang *et al.*, 2020) to analyse the response of the macroinvertebrate taxa to the different explanatory variables while accounting for taxa interactions. The key model fitting function was *manyglm*, which fits a separate GLM to each species using a common set of explanatory variables. The *anova* and *summary* functions, which work on *manyglm* objects in the same way as for *glm*, use resampling-based hypothesis testing to make community-level and taxon-specific inferences about which factors or environmental variables are associated with the multivariate abundances (Wang *et al.*, 2012). Multivariate test statistics calculated in *manyglm* analyses were constructed using a log-likelihood ratio statistic (LRT) (Warton *et al.*, 2012). To find which macroinvertebrate taxa were significantly affected by hydrological and spatial isolation we ran univariate tests for each species separately, by using the *p.uni="adjusted"* argument in the *anova* function, which results in a p-value calculated using 999 iterations.

3. RESULTS

3.1. Taxonomic and functional analysis

We collected a total of 8559 organisms, belonging to 85 taxa in 57 families (Supplementary Material, Appendix 1). There were on average 22 (± 11) taxa and 329 (± 318) individuals per site. The top three most abundant taxa were Orthocladiinae, *Caenis* and *Nemoura*, with mean relative abundances of 32, 9 and 6%, respectively. Macroinvertebrate communities were composed by a high abundance of Diptera (particularly Chironomidae) along all the hydrological gradient, as well as Trichoptera and Coleoptera.

The correlation results between functional and taxonomic metrics and hydrological and spatial isolation are shown in Table 2. Spearman's correlation coefficients (R^2) between these explanatory variables were very low (flow permanence vs closeness = 0.24; flow permanence vs surrounding water = -0.47 and closeness vs surrounding water = 0.16). The correlogram including canopy cover, all the sections of IHF and flow permanence (Supplementary Material, Appendix 4) revealed that canopy cover and the IHF global score were strongly correlated with flow permanence (R^2 = 0.59 and 0.72, respectively). Individually, the frequency of riffles (B2) and the habitat heterogeneity elements (B6) sections of the IHF also showed markedly positive correlations with flow permanence (R^2 = 0.74 and 0.67, respectively).

There were no detectable relationships between either functional or taxonomic metrics and surrounding water (Supplementary Material, Appendix 5a). On the contrary, flow permanence showed the strongest and most significant relationships with taxonomic and functional metrics. As we predicted, taxonomic richness (Fig. 7a) and functional richness (Fig. 7c) increased significantly with flow permanence ($p < 0.001$) and closeness (Fig. 7b and Fig. 7d, respectively; $p < 0.05$).

Table 2. Results of the GLM analyses relating taxonomic and functional metrics (see text for definitions) to hydrological isolation (flow permanence) and spatial isolation (closeness and surrounding water). Significance levels: *p < 0.05; **p < 0.01; ***p < 0.001.

	Flow permanence		**Log (Closeness)**		**Surrounding water**	
	Linear coefficient	R^2	Linear coefficient	R^2	Linear coefficient	R^2
% richness Chironomidae	-0.41***	0.45	-3.54	0.11	$-6.90 \cdot 10^{-4}$	$6.21 \cdot 10^{-3}$
% richness other Diptera	-0.31**	0.26	-3.94	0.13	$-1.37 \cdot 10^{-3}$	$2.47 \cdot 10^{-2}$
EPT	0.07**	0.34	0.58	0.09	$4.48 \cdot 10^{-5}$	$8.57 \cdot 10^{-3}$
OCH	0.11**	0.31	1.49*	0.19	$3.60 \cdot 10^{-4}$	$2.10 \cdot 10^{-2}$
Taxonomic richness	0.29***	0.43	3.09*	0.16	$4.57 \cdot 10^{-4}$	$5.02 \cdot 10^{-3}$
Functional richness	0.06***	0.47	0.61*	0.16	$-1.86 \cdot 10^{-5}$	$1.62 \cdot 10^{-4}$
Functional redundancy	0.16**	0.35	1.86*	0.15	$4.20 \cdot 10^{-4}$	$1.14 \cdot 10^{-2}$
Functional dispersion	$9.19 \cdot 10^{-3}$ **	0.36	0.11*	0.18	$-2.10 \cdot 10^{-6}$	$8.09 \cdot 10^{-5}$
Mean functional similarity	$-5.17 \cdot 10^{-3}$ **	0.25	-0.06	0.11	$-1.79 \cdot 10^{-5}$	$1.44 \cdot 10^{-2}$
Aerial active	-0.12	0.12	0.24	$1.45 \cdot 10^{-3}$	$1.70 \cdot 10^{-3}$	$1.04 \cdot 10^{-1}$
Aerial passive	-0.01	$3.81 \cdot 10^{-3}$	-0.25	$7.06 \cdot 10^{-3}$	$-1.72 \cdot 10^{-4}$	$4.87 \cdot 10^{-3}$
Aquatic active	-0.04	0.06	-0.40	$2.01 \cdot 10^{-2}$	$3.29 \cdot 10^{-5}$	$7.85 \cdot 10^{-3}$
Aquatic passive	0.18**	0.31	0.41	$5.45 \cdot 10^{-3}$	$-1.56 \cdot 10^{-3}$	$1.17 \cdot 10^{-1}$

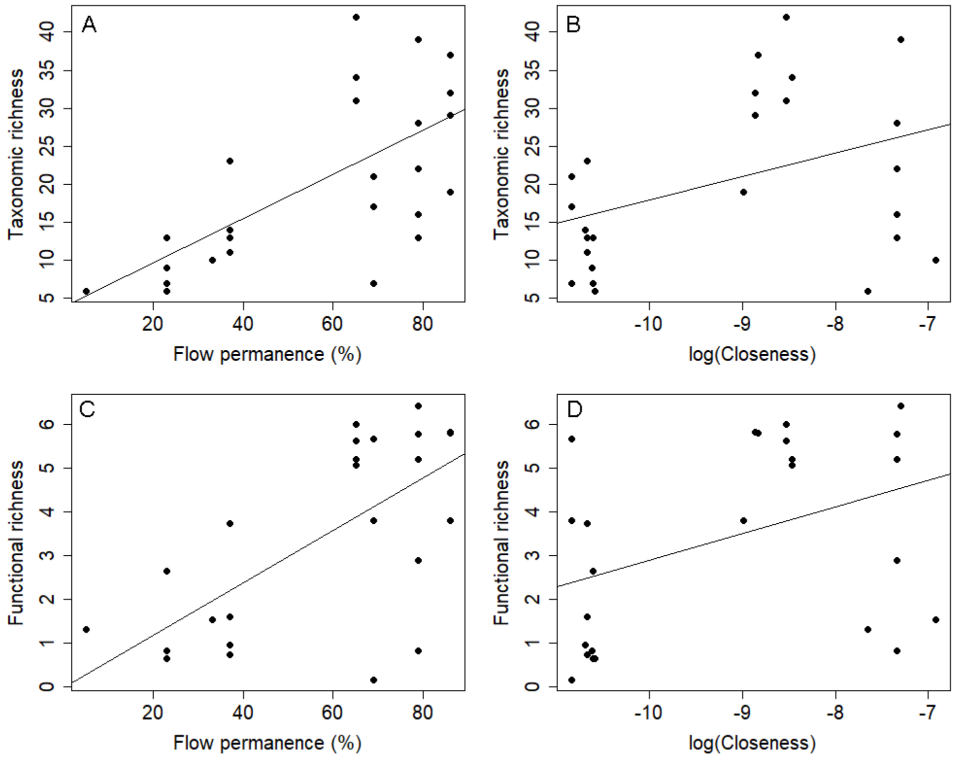

Figure 7. Plots showing the responses of taxonomic (a, b) and functional richness (c, d) to hydrological isolation (flow permanence: a, c) and spatial isolation (closeness: b, d). Solid lines represent the fitted values of generalized linear models (see Table 2).

EPT (Fig. 8a) and OCH (Fig. 8b) richness increased significantly with flow permanence ($p < 0.01$), whereas the % richness Chironomidae (Fig. 8c) and other Diptera (Fig. 8d) significantly decreased with flow permanence ($p < 0.001$ and $p < 0.01$, respectively). Closeness only had a significant and positive effect on OCH richness ($p < 0.05$).

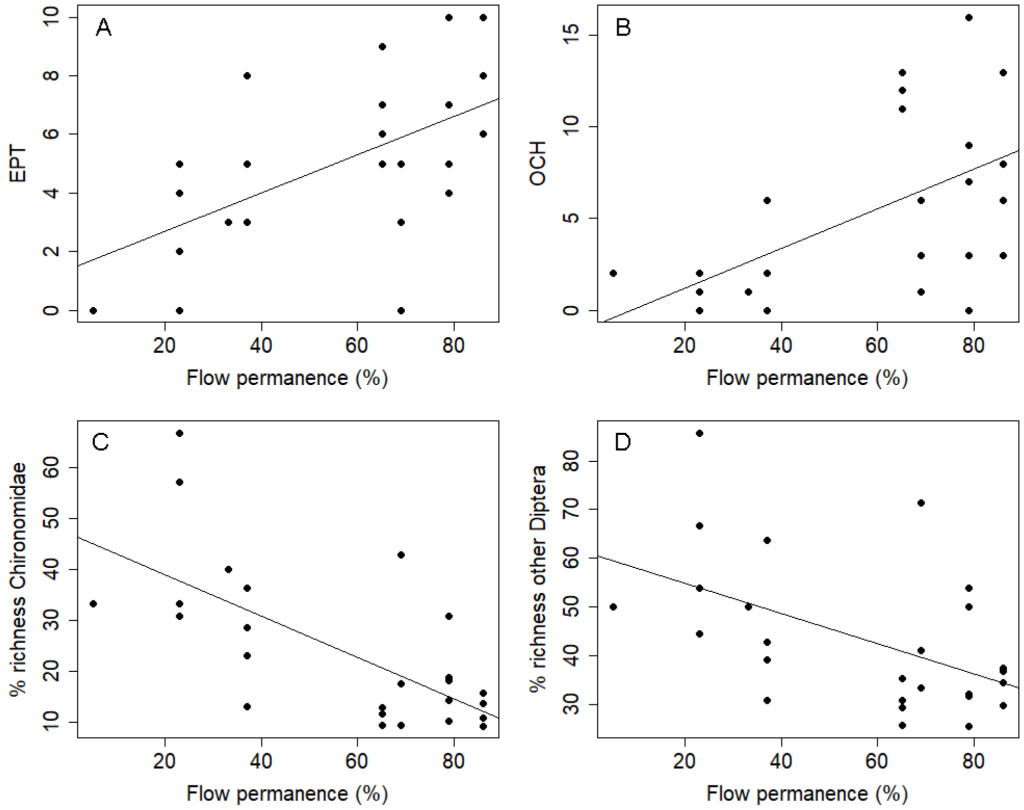

Figure 8. Plots showing the responses of taxonomic metrics to hydrological isolation (flow permanence): (a) EPT richness; (b) OCH richness; (c) % richness of Chironomidae taxa; (d) % richness other Diptera. Solid lines represent the fitted values of generalized linear models (see Table 2).

Regarding other functional variables at the community level, as we predicted, FR (Fig. 9a) and Fdis (Fig. 9c) increased with flow permanence ($p < 0.01$) and closeness (Fig. 9b and Fig. 9d, respectively; $p < 0.05$). At the taxon level, Fsim showed only a significant negative correlation with flow permanence (Fig. 9e; $p < 0.01$).

Analysis of multivariate abundance data revealed that there was a significant effect of hydrological isolation (LRT = 176.4, $p < 0.01$) on community composition, meaning that the taxonomic composition of macroinvertebrates clearly differs between the degree of flow permanence of each sampled stream. After adjusting for multiple testing, there was a significant and positive effect of flow permanence on *Oulimnius* ($p = 0.024$), *Gammarus* ($p = 0.019$) and Psychodidae ($p = 0.011$). In contrast, there was no significant effect of spatial isolation on macroinvertebrate community composition (closeness: LRT = 53.18, $p = 0.77$; surrounding water: LRT = 51.62, $p = 0.56$).

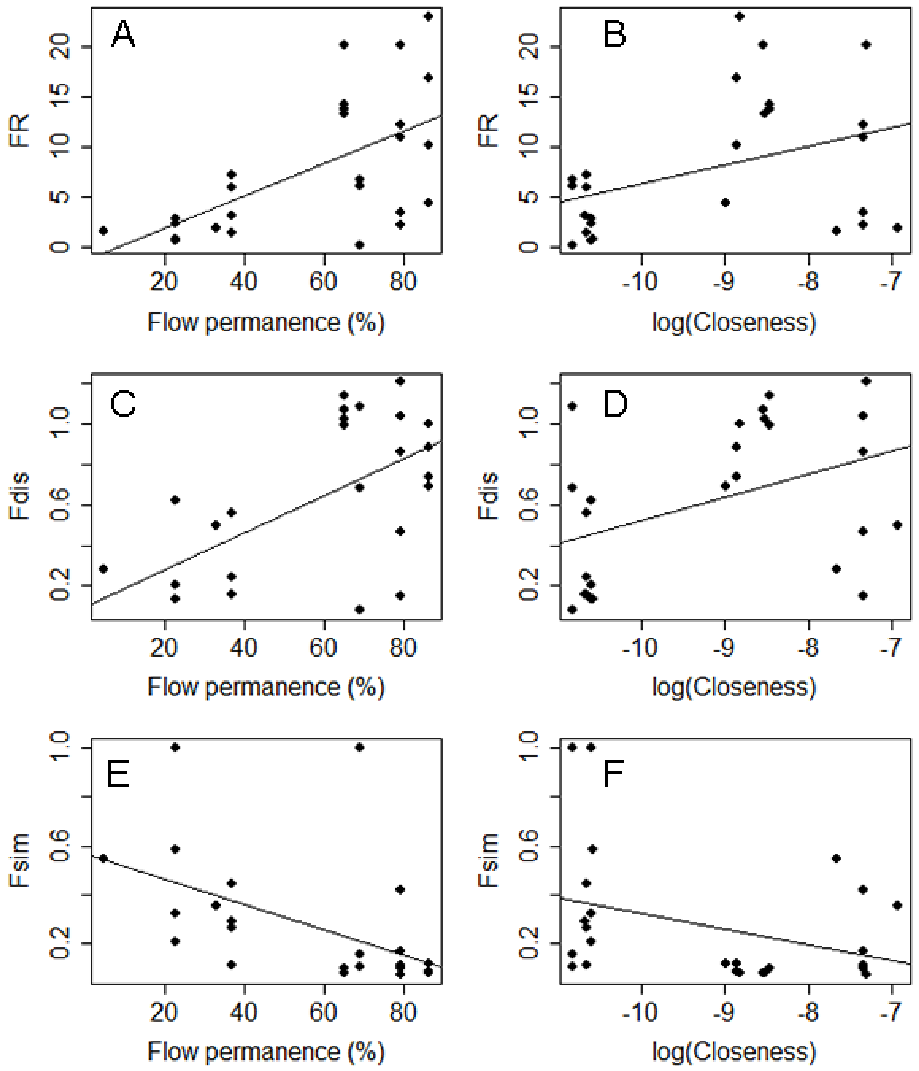

Figure 9. Plots showing the responses of functional metrics to hydrological isolation (flow permanence: a, c, e) and spatial isolation (closeness: b, d, f): (a, b) functional redundancy (FR); (c, d) functional dispersion (Fdis) and (e, f) mean functional similarity between taxa (Fsim). Solid lines represent the fitted values of generalized linear models (see Table 2). See Table 1 for a detailed description of each metric.

3.2. Macroinvertebrate dispersion analysis

There was no clear relationship between the relative abundance of the macroinvertebrate dispersion groups and the spatial isolation variables, both closeness (Fig. 10b, d, f, h) and surrounding water (Supplementary Material, Appendix 5b). In contrast, we detected an inverse relationship between aerial active and aquatic passive dispersal and flow permanence. Those sites with higher flow permanence had a significantly higher proportion of organisms that dispersed passively by streamflow (Fig. 10g; $p < 0.01$), whereas the most intermittent and ephemeral sites had a higher (but not significant) proportion of organisms that dispersed by flying (Fig. 10a; $p > 0.05$).

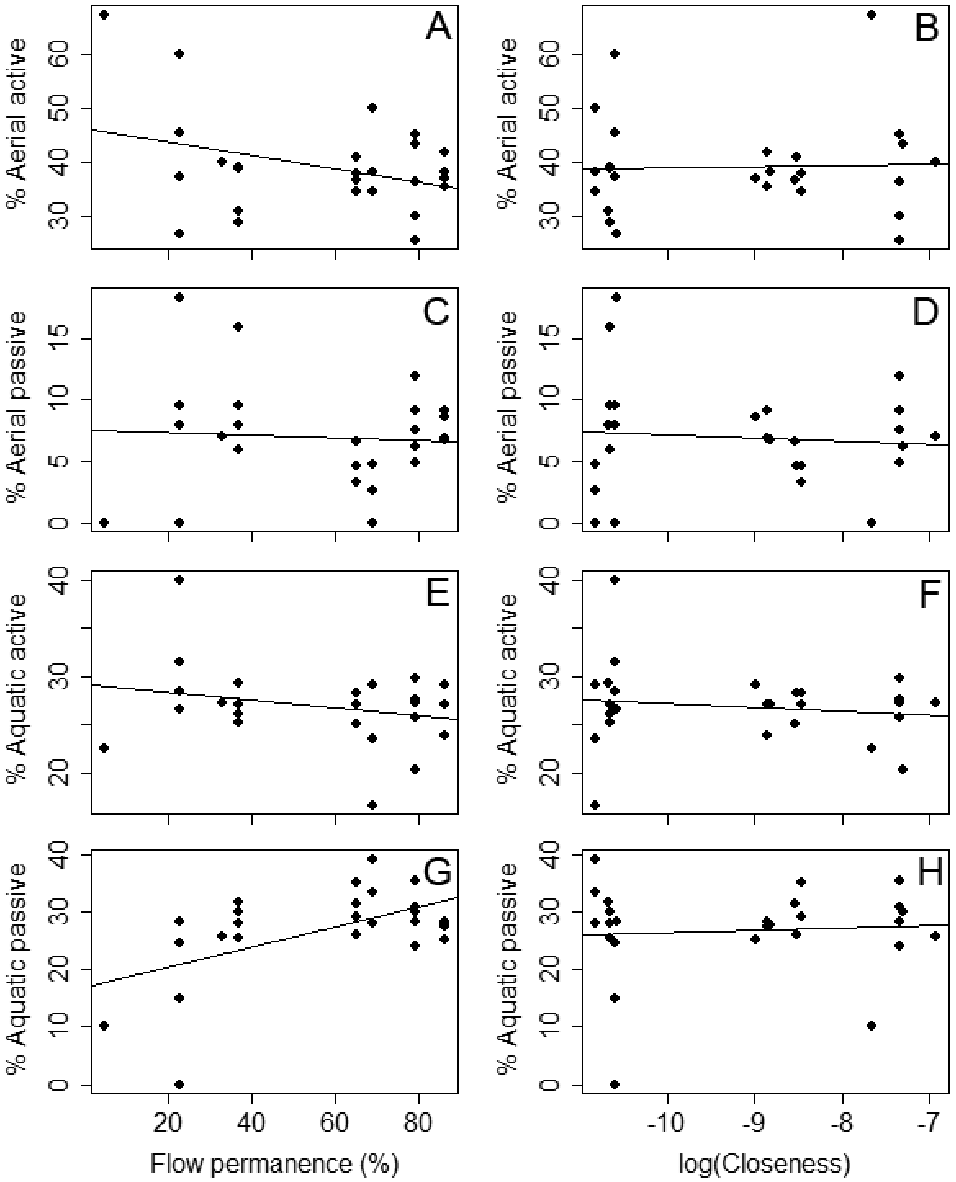

Figure 10. Plots showing the responses of dispersal traits to hydrological isolation (flow permanence; a, c, e, g) and spatial isolation (closeness; b, d, f, h): (a, b) % aerial active; (c, d) % aerial passive; (e, f) % aquatic active and (g, h) % aquatic passive dispersal. Solid lines represent the fitted values of generalized linear models (see Table 2).

4. DISCUSSION

4.1. Taxonomic and functional analysis

Understanding spatio-temporal variations of ecological communities in highly dynamic ecosystems is important in the context of climate change, which will increase the frequency and the duration of extreme events (Wolkovich *et al.*, 2014). Using IRES as models of highly dynamic ecosystems, we demonstrated significant effects of hydrological and spatial isolation on macroinvertebrate communities during the rewetting, and that hydrological isolation was much more important than spatial isolation.

Thus, as we predicted (**H1**), local hydrological conditions were more important than spatial connectivity for shaping aquatic macroinvertebrate communities in IRES during the rewetting. This agrees with Cañedo-Argüelles *et al.* (2020), who found that local hydrological conditions explained the highest proportion of community turnover in different streams of the Besòs and Llobregat catchments along 20 years.

In our study, we reported an increase of taxonomic and functional richness with flow permanence during the rewetting (**H2** and **H4**), in agreement with previous studies that analysed richness patterns during other hydrological periods (e.g., Bonada *et al.*, 2007; Stubbington *et al.*, 2009; Datry *et al.*, 2014b; Schriever *et al.*, 2015; Soria *et al*., 2017). Moreover, we found that the most perennial sites had higher canopy cover and IHF values (especially, more frequency of riffles and heterogeneity elements such as presence of leaves and wood), thus favouring the availability of refugia and substrate diversity. These sites could support a higher number of habitats to be occupied for different species (Bonada *et al.*, 2007). In this sense, we observed significant positive correlations between EPT and OCH richness and flow permanence (**H3**). EPT and OCH metrics are good indicators of the seasonal changes in macroinvertebrate communities in Mediterranean streams (Rieradevall *et al.*, 1999; Bonada *et al.*, 2006). EPT are more abundant during the wet season but some may be replaced by OCH in summer (Williams, 1996). We hypothesised higher values of OCH in the most intermittent and ephemeral sites since OCH has been known as a good indicator of flow intermittence (Bonada *et al.*, 2006), but this hypothesis (**H3**) was rejected with our results. These contradictory results could be due to samples that were collected in autumn (i.e., the rewetting period), and not during spring or summer when this metric is widely used and works appropriately. Recolonisation of Coleoptera and Hemiptera taxa to IRES with flow resumption could be possible since they could fly as aerial adults, although the loss of longitudinal connectivity differs from typical community patterns and processes of spring-summer (Bonada *et al.*, 2006, Bogan & Boersma, 2012). Contrarily, other taxa with desiccation-sensitive aquatic juveniles such as Odonata could not fly from perennial waters at the moment when we sampled because Odonata require more time in the water to emerge, so they could not have the sufficient time to recolonise the intermittent reaches (Bogan *et al.*, 2015).

On the contrary, as we predicted (**H3**), macroinvertebrate communities of more intermittent and ephemeral streams were dominated by Chironomidae and other Diptera, and some genera of Coleoptera and Hemiptera. Aspin *et al.* (2018) also found an increase in % richness of non-Chironomidae Diptera with drought intensity. Some

Diptera families (e.g., Ceratopogonidae, Limoniidae, Simuliidae) and Chironomidae taxa (e.g., Orthocladiinae, Tanytarsini) are drought specialists and ubiquitous with short life cycles, constituting a highly tolerant group of stream insects that can persist in the dwindling pools (Boulton & Lake, 2008) or survive in isolated water bodies during periods of no flow (Cañedo-Argüelles *et al.*, 2016). Consequently, these macroinvertebrate taxa are present throughout the year (Langton & Casas, 1999; Rieradevall *et al.*, 1999; Bogan & Lytle, 2007) and their relative richness and relative abundance increase in IRES during the early phases of rewetting.

Analysis of multivariate abundance showed a significant correlation between flow permanence and taxonomic macroinvertebrate composition. This approximation confirmed the results of the individual GLM regressions conducted, indicating that flow permanence was a primary driver of macroinvertebrate communities and meta-communities, as other authors reported before (e.g., Arscott *et al.*, 2010, Datry *et al.*, 2014b, Schriever *et al.*, 2015; Cañedo-Argüelles *et al.*, 2020). Furthermore, the multivariate analysis revealed that *Gammarus*, *Oulimnius* and Psychodidae abundances were significantly correlated with flow permanence. Vadher *et al.* (2018a) demonstrated that *Gammarus pulex* survivorship was reduced linearly with increasing drying duration, with a 70% of mean survivorship following 21 days of drying at the laboratory scale and a 51% at the field-scale (Vadher *et al.*, 2018b). Differently, Psychodidae is considered a specialist taxon appearing rapidly after rewetting of a dry site (Aspin *et al.*, 2018), while *Oulimnius* is a strong indicator of streams with pool-riffle sequences (Milner *et al.*, 2015).

Regarding functional metrics at the taxon level (**H4**), we found lower Fsim as flow permanence increased. This result agrees with those observed in Gutiérrez-Cánovas *et al.* (2015), where anthropogenic and natural stressors caused higher functional community similarity. Previous studies indicated that habitat filtering reduces overdispersion for each trait, producing a convergence toward the optimum value (Shipley *et al.*, 2006, Weiher *et al.*, 2011). Alternatively, functional metrics at the whole-community level revealed that sites with higher flow permanence and closeness had higher values of Fdis, FR and functional richness (as we mentioned before). Previous studies suggested that there are inherently high levels of functional redundancy in IRES (Boersma *et al.*, 2014; Schriever *et al.*, 2015; Vander Vorste *et al.*, 2016; Leigh *et al.*, 2019) due to harsh environmental conditions that may exclude taxa poorly adapted to these conditions, yielding communities comprised of disturbance-resistant and/or resilient taxa (Mouchet *et al.*, 2010). Therefore, the most perennial streams, with less hydrological and spatial isolation, had more functional niche space occupied, and more dominant species located further from the centre (higher Fdis), suggesting greater interspecific competition between taxa and higher resilience to environmental changes because of niche complementarity (Schriever *et al.*, 2015). However, these significant trends between hydrological and spatial isolation metrics and functional features could be related with the probability of finding more or fewer trait categories solely because of the number of taxa (i.e., sampling effect) (Gutiérrez-Cánovas *et al.*, 2015).

4.2. Macroinvertebrate dispersion analysis

In IRES, every taxon that persists must possess resistance and/or resilience adaptations to cope with flow intermittence (Nimmo *et al.*, 2015). The sampled area in this study was mainly composed by bedrock-dominated headwater IRES that might not allow for drought-resistance strategies to be developed by macroinvertebrates (Folch, 2020). This type of IRES lacks hyporheic communities and relies more on resilience traits for faunal recovery (e.g., Bogan *et al.*, 2015; Chester *et al.*, 2015). During drying periods, the most favourable resilient strategy for the aquatic insects is to fly to perennial refuges (Cañedo-Argüelles *et al.*, 2015). However, the analysis of the dispersal traits during the rewetting did not reveal a significantly higher % of aerial dispersal organisms arriving from these refugia. Conversely, we observed a significant positive correlation between flow permanence and aquatic passive dispersal (**H5**). Flow resumption during the rewetting allows the longitudinal connectivity, being more feasible the aquatic dispersal by active or passive drift. Active drift is usually limited to short, within-riffle distances (Lancaster *et al.*, 2011; Naman *et al.*, 2016) but passive drift could be very important with possible long-distance dispersal events during major floods (i.e., catastrophic drift which is related to discharge intensity rather than to species' drifting propensities) (Sarremejane *et al.*, 2017a). It is reasonable to think that the flash floods occurred upon rewetting could allow these large dispersal events by drift, explaining why the sites with more closeness value (i.e., more connectivity through the river network) had higher taxonomic and functional richness. In contrast, we did not find any significant correlation between community metrics and surrounding water. This result could support the fact that the recolonisation to the rewetted habitats was mainly happening along the stream network and not overland. Therefore, recolonising organisms could arrive from upstream perennial refuges or from upstream isolated pools that remained through the drying period. Similarly, we found a significant positive correlation between OCH richness and closeness, so increased closeness would increase the chances of OCH to disperse through the stream network from nearby perennial waters (upstream or downstream). Some taxa such as Coleoptera (e.g., adult Dytiscidae) are strong aerial dispersers (Bogan & Boersma, 2012), being able to detect polarised light reflecting from the water surface (Schwind, 1991), thus favouring their dispersal through the stream network. For example, the diving beetle *Agabus* (Dytiscidae) which was identified in half of samples is often one of the first predators to aerially colonise intermittent streams upon rewetting (Bogan, 2012).

4.3. Singularities of rewetting

Rewetting and drying patterns in IRES are often asynchronous and occur across multiple spatial extents (Stanley *et al.*, 1997), which converts them to highly dynamic ecological systems (Datry *et al.*, 2016) with continuous changes in biological communities (Fig. 1). Therefore, community patterns and processes from a particular period might not be applicable to other periods. Consequently, the results obtained in our study are specific to the rewetting, mainly during early autumn in Mediterranean climate regions. Most studies in IRES have focused on the drying period, where streams contracts and the loss of longitudinal connectivity influence community patterns and processes. An analysis of trait dispersion during this period would have likely shown, for example, a significant negative correlation between flow permanence and % aerial dispersal. Specialist predators with strong flying abilities such as OCH rapidly colonise the remaining pools of streams (Fig. 1) (Bogan & Boersma, 2012), so OCH richness would have also decreased with flow permanence. Moreover, as longitudinal connectivity is lost during drying, dispersion through the river network would be lower than that reported during the rewetting since drift dispersal would be limited (Bogan *et al.*, 2013). In contrast, surrounding water would have more importance on macroinvertebrate dispersion, favouring higher overland dispersal by OCH and other flying macroinvertebrates that use nearby perennial refuges (Cañedo-Argüelles *et al.*, 2015).

5. CONCLUSIONS

The main conclusions reached can be sum up on the following seven points:

1) A strong and significant effect of antecedent hydrological isolation (flow permanence) on macroinvertebrate taxonomic richness and other functional features (functional richness, Fdis, FR and Fsim) during the rewetting.

2) A progressive taxonomic shift from poor-communities dominated by Chironomidae and other Diptera in the most intermittent and ephemeral sites with a high Fsim towards a greater presence of EPT and OCH richness in most perennial sites, and therefore higher functional richness.

3) Spatial isolation significantly determined the recolonisation of macroinvertebrates to the rewetted sites even in the fine-scale studied in this work, and that closeness was significantly correlated with taxonomic and functional richness, FR, Fdis and OCH richness.
4) A higher importance of aquatic passive dispersal in sites with lower hydrological isolation.
5) The position of the sites at the subcatchment scale could favour the recolonisation of drifting and flying macroinvertebrate colonists (e.g., Coleoptera and Hemiptera) through the stream network (the main dispersal pathway). In this regard, the previous flood events before sampling could have allowed important long-distance dispersal events by drift dispersal through the river network.
6) Surrounding water did not show any significant correlation with any macroinvertebrate variable tested, so aerial recolonisation through overland dispersal from nearby perennial refuges was not important.
7) IRES are dynamic and shifting habitat mosaics (Fig. 1) and thus all the results shown in our study are specific for the rewetting period and need to be compared with other seasons that show different stream network topologies and local hydrological conditions.

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8. SUPPLEMENTARY MATERIAL

Appendix 1. Taxa list by groups

Group	Taxa
Amphipoda	Gammarus
Bilvalvia	Sphaerium
Coleoptera	Agabus
Coleoptera	Coelostoma
	Cyphon
	Deronectes
	Dryops
	Dytiscus
	Elmis
	Elodes
	Gyrinus
	Haliplus
	Hydraena
	Hydrochara
	Hydrocyphon
	Hydrophilus
	Meladema
	Laccobius
	Laccophilus
	Limnebius
	Limnius
	Peltodytes
	Oulimnius
	Riolus
	Stictonectes
Decapoda	Palaemonidae
Diptera	Anthomyidae
	Athericidae
	Ceratopogonidae
	Chironomini
	Culicidae
	Dixidae
	Empididae
	Limoniidae
	Orthocladiinae
	Psychodidae
	Sciomyzidae
	Simuliidae
	Stratiomyidae
	Syrphidae
	Tabanidae
	Tanypodinae
	Tanytarsini

Group	Taxa
	Thaumalidae
	Tipulidae
Ephemeroptera	Baetis
	Caenis
	Cloeon
	Electrogena
	Habrophlebia
Gastropoda	Lymnaea
	Gyraulus
	Physa
	Radix
Hemiptera	Corixa
	Hydrometra
	Micronecta
	Naucoris
	Notonecta
	Velia
Hydracarina	Hydracarina
Megaloptera	Sialis
Odonata	Anax
	Boyeria
	Calopteryx
	Coenagrion
	Cordulegaster
	Gomphus
	Ischnura
	Onychogomphus
	Orthetrum
	Platycnemis
	Pyrrhosoma
	Sympetrum
Oligochaeta	Oligochaeta
Plecoptera	Nemoura
Trichoptera	Hydropsyche
	Hydroptila
	Limnephilus
	Mystacides
	Odontocerum
	Philopotamus
	Polycentropus
	Stactobia
	Tinodes

Appendix 2: Environmental characteristics of the different sampling sites. Aquatic states describe the availability of mesohabitats occurring on a given reach at a particular moment, depending on the hydrological conditions (Gallart *et al.*, 2012). B1-B7 are the seven sections of "Índice de Hábitat Fluvial" (IHF) used here as a surrogate for instream habitat heterogeneity (Pardo *et al.*, 2004): (B1) the substrate inclusion in riffles and sedimentation in pools; (B2) the frequency of riffles; (B3) the substrate diversity; (B4) the flow velocity and depth regime; (B5) the shade percentage in the channel; (B6) the habitat heterogeneity elements and (B7) the aquatic vegetation coverage. The IHF column represents the global score (the sum of all the sections).

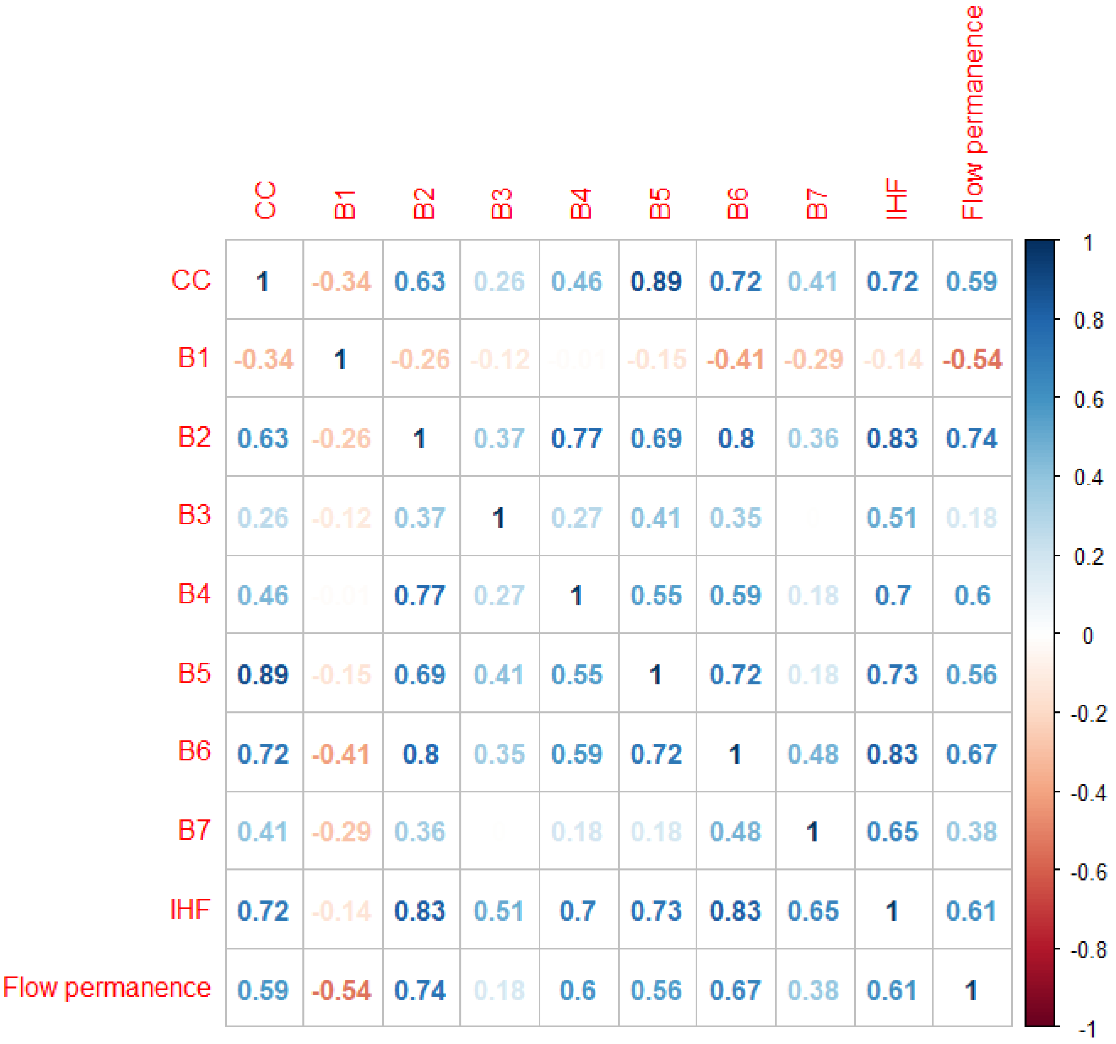
Stream	Site	pH	Oxygen (mg/l)	Oxygen (%sat)	Temperature (ºC)	Conductivity (microS/cm)	Suspended solids (mg/l)	Canopy coverage	Streamflow (l/s)	Aquatic state	B1	B2	B3	B4	B5	B6	B7	IHF
Talamanca	T1	8.01	12.72	100.60	5.30	610.00	396.50	10	1.16	Eurheic	10	6	14	8	3	6	20	67
Talamanca	T2	8.08	13.12	106.20	6.20	535.20	347.10	0	0.00	Oligorheic	5	4	15	6	3	4	10	47
Talamanca	T3	8.19	13.52	101.20	3.30	558.80	362.70	1	0.16	Oligorheic	10	4	15	6	3	4	20	62
Talamanca	T4	7.65	7.79	62.50	6.20	561.50	364.00	15	0.01	Oligorheic	5	4	17	0	3	6	20	55
Santa Creu	SC1	7.78	8.67	70.90	6.70	792.00	513.50	1	0.00	Arheic	10	2	15	6	3	2	10	48
Santa Creu	SC2	8.01	11.54	99.50	8.70	858.00	559.00	1	0.00	Arheic	10	2	15	4	3	4	10	48
Santa Creu	SC3	8.07	11.50	92.00	5.70	877.00	572.00	0	0.00	Arheic	5	0	20	4	3	4	10	46
Santa Creu	SC4	7.95	11.58	107.00	11.70	839.00	546.00	1	0.00	Arheic	10	2	15	6	3	6	15	57
Rellinars	R4	8.29	13.39	100.00	3.10	622.40	404.30	5	0.30	Oligorheic	10	4	12	8	3	4	10	51
Mura	MU2	7.94	10.68	88.20	7.10	584.40	380.25	65	1.82	Arheic	10	6	17	8	10	8	20	79
Mura	MU3	8.14	12.80	97.00	3.60	596.80	388.06	25	2.40	Eurheic	5	6	17	8	3	6	15	60
Mura	MU4	7.93	12.40	94.40	3.90	586.20	380.25	15	1.27	Eurheic	5	6	14	8	3	8	15	59
Gaià	G1	8.00	9.07	70.10	4.50	536.60	348.10	40	0.00	Arheic	5	2	14	4	3	6	20	54
San Ana	SA1	7.68	9.29	80.90	9.30	645.10	419.25	65	3.81	Eurheic	5	6	12	8	5	8	30	74
San Ana	SA2	7.97	10.90	93.60	8.70	654.95	424.45	10	2.43	Eurheic	5	6	20	8	3	8	25	75
San Ana	SA3	8.02	11.51	95.50	7.30	664.00	431.60	70	1.41	Eurheic	5	8	17	8	10	8	15	71
San Ana	SA4	8.00	11.29	93.70	7.40	652.30	424.45	1	0.82	Eurheic	5	6	12	8	3	6	20	60
San Ana	SA5	8.28	13.75	108.20	5.20	661.50	430.95	1	1.96	Oligorheic	5	4	15	6	3	6	10	49
Vall d'Horta	H1	7.80	9.95	82.00	7.00	685.20	445.25	80	13.37	Eurheic	5	8	20	10	10	10	20	83
Vall d'Horta	H2	7.87	11.03	89.30	6.40	702.80	454.35	70	1.18	Eurheic	5	8	20	10	10	10	20	83
Vall d'Horta	H3	7.60	10.07	84.60	7.80	696.00	452.40	70	1.38	Arheic	5	10	20	10	10	10	20	85
Vall d'Horta	H5	7.89	10.91	92.60	8.20	607.40	395.20	50	0.53	Oligorheic	5	4	17	6	5	4	15	56
Castelló	CA1	8.25	11.27	89.10	5.40	690.30	448.50	10	0.24	Oligorheic	5	4	10	6	3	6	20	54
Castelló	CA2	8.01	12.01	97.70	6.50	593.20	386.75	45	0.12	Oligorheic	5	4	12	6	5	6	30	68
Castelló	CA3	7.88	11.26	92.30	6.80	696.60	453.70	20	0.06	Oligorheic	5	4	17	6	3	6	30	71
Castelló	CA4	8.16	13.86	108.70	5.10	527.80	343.85	40	0.00	Arheic	5	2	7	4	5	6	15	44

Appendix 3: List of traits and modalities for taxa from our dataset from Tachet *et al.* (2010) used in functional analyses.

	Maximal size							Life cycle duration		Potential number of reproduction cycles			Aquatic stages				Reproduction								Dissemination				Resistance form					Respiration					Locomotion and substrate relation								Food									Feeding habits							
	≤.25 cm	>.25-.5 cm	>.5-1 cm	>1-2 cm	> 2-4 cm	>4-8 cm	>8 cm	≤ 1 year	>1 year	<1	1	>1	egg	larva	nymph	imago	Ovoviviparity	Isolated eggs, free	Isolated eggs, cemented	Clutches, cemented or fixed	Clutches, free	Clutches in vegetation	Clutches, terrestrial	Asexual reproduction	Aquatic passive	Aquatic active	Aerial passive	Aerial active	Eggs, statoblasts, gemmules	Cocoons	Cells against desiccation	Diapause or dormancy	None	Tegument	Gill	Plastron	Spiracle (aerial)	Hydrostatic vesicle (aerial)	Flier	Surface swimmer	Swimmer	Crawler	Burrower (epibenthic)	Interstitial (endobenthic)	Temporarily attached	Permanently attached	Fine sediment + microrganisms	Detritus < 1 mm	Plant detritus ≥ 1 mm	Living microphytes	Living macrophytes	Dead animal > 1 mm	Living microinvertebrates	Living macroinvertebrates	Vertebrates	Absorber	Deposit feeder	Shredder	Scraper	Filter-feeder	Piercer (plant or animal)	Predator	Parasite, parasitoid
	a1	a2	a3	a4	a5	a6	a7	b1	b2	c1	c2	c3	d1	d2	d3	d4	e1	e2	e3	e4	e5	e6	e7	e8	f1	f2	f3	f4	g1	g2	g3	g4	g5	j1	j2	j3	j4	j5	u1	u2	u3	u4	u5	u6	u7	u8	h1	h2	h3	h4	h5	h6	h7	h8	h9	i1	i2	i3	i4	i5	i6	i7	i8
Agabus	0	0	3	2	0	0	0	0	3	0	3	1	3	3	0	2	0	0	0	3	0	1	0	0	1	1	0	3	0	0	0	0	3	1	0	0	3	0	1	0	3	3	0	0	0	0	0	0	0	0	0	0	1	3	1	0	0	3	0	0	3	0	0
Anax	0	0	0	0	0	3	0	2	2	1	3	0	2	3	0	0	0	0	0	0	0	3	2	0	0	1	0	3	2	0	0	2	2	1	3	0	0	0	0	0	2	4	0	0	0	0	0	0	0	0	0	0	1	4	1	0	0	0	0	0	0	3	0
Baetis	0	0	3	1	0	0	0	3	0	0	2	3	3	3	0	0	0	0	1	3	0	0	0	0	3	2	1	3	2	0	0	0	2	1	2	0	0	0	0	0	3	4	0	1	0	0	0	2	2	5	1	1	0	0	0	0	1	0	3	0	0	0	0
Boyeria	0	0	0	0	3	1	0	0	3	3	0	0	2	3	0	0	0	0	0	0	0	3	0	0	2	0	0	3	0	0	0	1	3	1	3	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	1	4	1	0	0	0	0	0	0	3	0
Caenis	0	2	3	0	0	0	0	3	0	0	1	3	3	3	0	0	0	1	2	0	0	0	0	0	2	1	1	1	2	0	0	1	2	1	3	0	0	0	0	0	0	5	1	1	0	0	1	4	2	1	1	1	0	0	0	0	3	1	0	0	0	0	0
Calopteryx	0	0	0	1	3	1	0	2	2	1	3	0	3	3	0	0	0	0	0	0	0	3	0	0	2	1	0	2	0	0	0	2	2	1	3	0	0	0	0	0	1	4	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	3	0
Cloeon	0	0	3	0	0	0	0	3	0	0	1	3	3	3	0	0	3	1	1	0	0	0	0	0	1	2	1	2	0	0	0	0	3	1	2	0	0	0	0	0	3	1	0	0	0	0	0	3	1	3	1	0	1	0	0	0	3	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	1	1	0	3	0	0	0	0	3	1	0	1	3	0	1	0	3	3	0	0	0	0	0	0	0	3	0	0	3	1	0	0	3	2	0	0	0	1	0
Coenagrion	0	0	0	3	0	0	0	3	1	1	3	1	2	3	0	0	0	0	0	0	0	3	0	0	2	1	0	3	0	0	0	2	2	1	3	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	1	4	0	0	0	0	0	0	0	3	0
Cordulegaster	0	0	0	0	2	3	0	0	3	3	0	0	2	3	0	0	0	3	0	0	0	0	1	0	2	0	0	3	0	0	0	0	3	1	3	0	0	0	0	0	0	1	4	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	3	0
Corixa	0	0	2	3	0	0	0	3	0	0	3	2	3	3	0	2	0	0	1	2	0	1	0	0	0	3	1	3	0	0	0	1	0	1	0	2	3	0	1	0	5	0	0	0	0	0	0	0	1	2	1	2	3	0	0	0	0	1	1	0	3	0	0
Cyphon	0	3	0	0	0	0	0	1	3	0	3	0	3	3	0	0	0	0	0	0	0	0	3	0	0	1	0	3	0	0	0	0	3	1	3	0	0	0	0	0	0	5	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	1	3	0	0	0	0
Deronectes	0	3	1	0	0	0	0	1	3	0	1	3	3	3	0	2	0	0	0	3	0	0	0	0	2	1	0	3	0	0	0	0	3	1	0	0	3	0	1	0	3	3	0	0	0	0	0	0	0	0	0	0	2	3	0	0	0	3	0	0	3	0	0
Dryops	0	3	0	0	0	0	0	1	3	0	3	0	1	2	0	1	0	0	0	0	0	1	3	0	0	1	0	3	0	0	0	0	3	3	0	3	3	0	2	0	0	3	3	0	0	0	0	0	3	3	0	0	0	0	0	0	0	3	3	0	0	0	0
Dugesia	0	0	1	2	3	0	0	0	3	0	3	0	3	3	0	3	0	0	0	2	0	0	0	2	0	2	0	0	0	2	0	0	1	3	0	0	0	0	0	1	0	5	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	3	0
Dytiscus	0	0	0	0	3	1	0	0	3	0	3	0	3	3	0	2	0	0	0	0	0	3	0	0	0	1	0	3	0	0	0	0	3	1	0	0	3	0	1	0	3	3	0	0	0	0	0	0	0	0	0	0	0	3	3	0	0	3	0	0	3	0	0
Electrogena	0	0	0	3	0	0	0	3	0	0	3	0	3	3	0	0	0	1	2	0	0	0	0	0	3	1	1	3	2	0	0	1	2	1	3	0	0	0	0	0	1	5	0	0	0	0	0	3	1	3	0	0	0	0	0	0	0	0	3	0	0	0	0
Elmis	0	3	0	0	0	0	0	1	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	0	1	0	0	4	0	1	0	0	0	1	0	3	0	0	0	0	0	0	0	1	3	0	0	0	0
Elodes	0	3	0	0	0	0	0	1	3	0	3	0	3	3	0	0	0	0	0	0	0	0	3	0	1	1	0	3	0	0	0	0	3	1	3	0	0	0	0	0	0	5	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	1	3	0	0	0	0
Gammarus	0	0	0	2	2	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	0	0	0	2	3	0	1	0	0	0	1	5	2	1	2	2	1	0	0	0	3	1	0	0	0	0
Gomphus	0	0	0	0	3	0	0	0	3	3	0	0	3	3	0	0	0	1	3	0	0	0	0	0	2	0	0	3	3	0	0	0	0	1	3	0	0	0	0	0	0	1	4	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	3	0
Gyraulus	0	0	3	0	0	0	0	3	1	0	3	0	3	0	0	3	0	0	0	3	0	0	0	0	2	2	0	0	0	0	0	1	1	3	0	0	0	0	0	1	0	3	0	0	0	0	0	0	1	4	1	1	0	0	0	0	0	1	3	0	0	0	0
Gyrinus	0	2	3	0	0	0	0	1	3	0	3	0	3	3	0	2	0	0	0	3	0	0	0	0	0	2	0	3	0	0	0	0	3	1	3	0	3	0	1	3	3	3	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	3	0	0	3	0	0
Habrophlebia	0	0	3	0	0	0	0	3	0	0	3	0	3	3	0	0	0	1	3	0	0	0	0	0	1	1	1	1	2	0	0	1	1	1	3	0	0	0	0	0	1	3	0	0	0	0	0	1	3	3	0	0	0	0	0	0	1	3	0	0	0	0	0
Haliplus	0	3	0	0	0	0	0	1	3	0	1	3	3	3	0	2	0	0	0	0	0	3	0	0	1	1	0	3	0	0	0	0	3	3	0	0	3	0	1	0	3	3	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	3	0	0
Hydraena	0	3	0	0	0	0	0	1	3	0	3	1	3	0	0	3	0	0	0	0	0	0	3	0	2	1	0	3	0	0	0	0	3	0	0	3	2	0	1	0	3	3	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	1	3	0	0	0	0
Hydrocyphon	2	2	0	0	0	0	0	1	3	0	3	0	3	3	0	0	0	0	0	0	0	0	3	0	2	1	0	3	0	0	0	0	3	1	3	0	0	0	0	0	0	5	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	1	3	0	0	0	0
Hydrometra	0	0	1	3	0	0	0	3	0	0	3	1	0	2	0	2	0	0	1	0	0	3	0	0	1	3	0	1	0	0	0	3	0	0	0	0	3	0	1	4	0	2	0	0	0	0	0	0	0	0	0	3	3	1	0	0	0	0	0	0	3	0	0
Hydrophilus	0	0	0	0	2	3	0	0	3	0	3	1	3	3	0	2	0	0	0	0	3	0	0	0	0	1	0	3	0	0	0	0	3	1	0	2	3	0	1	0	3	3	0	0	0	0	0	0	0	0	1	0	1	3	0	0	0	3	0	0	0	1	0
Hydropsyche	0	0	1	3	1	0	0	3	0	0	2	2	3	3	3	0	0	0	0	3	0	0	0	0	3	2	1	3	0	0	0	0	3	2	3	0	0	0	0	0	0	2	0	0	3	0	0	2	1	3	0	0	3	1	0	0	0	0	0	3	0	1	0
Hydroptila	0	3	1	0	0	0	0	3	0	0	2	3	3	3	3	0	0	0	0	3	0	0	0	0	1	1	2	1	0	0	0	0	3	3	1	0	0	0	0	0	0	3	0	0	1	0	0	2	0	1	4	0	0	0	0	0	1	1	1	0	3	0	0

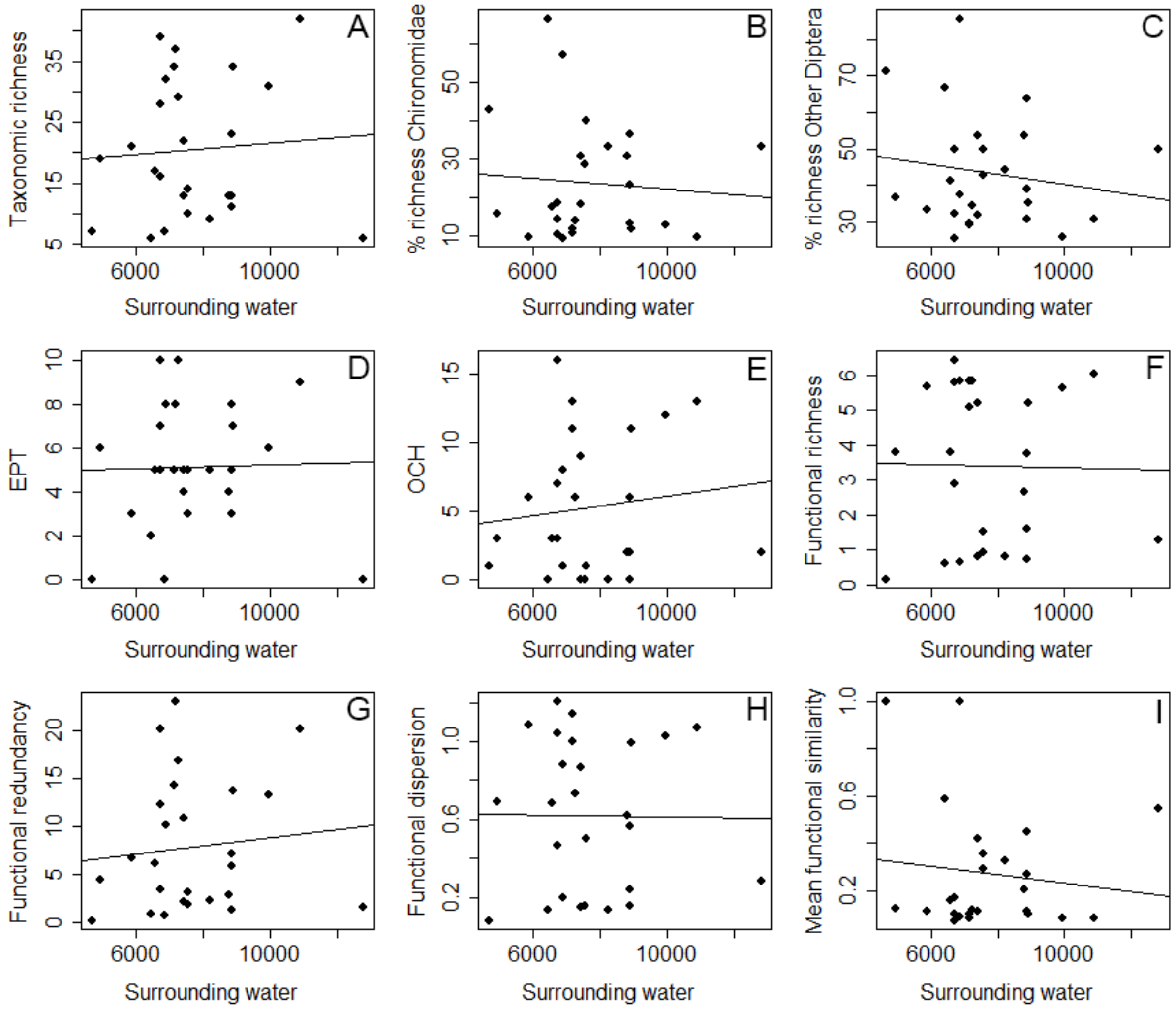
	Maximal size							Life cycle duration		Potential number of reproduction cycles			Aquatic stages				Reproduction								Dissemination				Resistance form					Respiration					Locomotion and substrate relation								Food									Feeding habits							
	≤.25 cm	> .25-.5 cm	> .5-1 cm	>1-2 cm	> 2-4 cm	>4-8 cm	>8 cm	≤ 1 year	>1 year	<1	1	>1	egg	larva	nymph	imago	Ovoviviparity	Isolated eggs, free	Isolated eggs, cemented	Clutches, cemented or fixed	Clutches, free	Clutches in vegetation	Clutches, terrestrial	Asexual reproduction	Aquatic passive	Aquatic active	Aerial passive	Aerial active	Eggs, statoblasts, gemmules	Cocoons	Cells against desiccation	Diapause or dormancy	None	Tegument	Gill	Plastron	Spiracle (aerial)	Hydrostatic vesicle (aerial)	Flier	Surface swimmer	Swimmer	Crawler	Burrower (epibenthic)	Interstitial (endobenthic)	Temporarily attached	Permanently attached	Fine sediment + microorganisms	Detritus < 1 mm	Plant detritus ≥ 1 mm	Living microphytes	Living macrophytes	Dead animal > 1 mm	Living microinvertebrates	Living macroinvertebrates	Vertebrates	Absorber	Deposit feeder	Shredder	Scraper	Filter-feeder	Piercer (plant or animal)	Predator	Parasite, parasitoid
	a1	a2	a3	a4	a5	a6	a7	b1	b2	c1	c2	c3	d1	d2	d3	d4	e1	e2	e3	e4	e5	e6	e7	e8	f1	f2	f3	f4	g1	g2	g3	g4	g5	j1	j2	j3	j4	j5	u1	u2	u3	u4	u5	u6	u7	u8	h1	h2	h3	h4	h5	h6	h7	h8	h9	i1	i2	i3	i4	i5	i6	i7	i8
Ischnura	0	0	0	3	0	0	0	3	0	0	2	2	2	3	0	0	0	0	0	0	0	3	0	0	1	1	0	3	0	0	0	2	2	1	3	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	1	4	0	0	0	0	0	0	0	3	0
Laccobius	0	3	0	0	0	0	0	1	3	0	3	1	3	3	0	2	0	0	0	3	0	0	0	0	1	1	0	3	0	0	0	0	3	1	0	1	3	0	1	0	3	3	0	0	0	0	0	0	0	3	0	0	3	1	0	0	0	3	0	0	0	1	0
Laccophilus	0	3	0	0	0	0	0	0	3	0	3	1	3	3	0	2	0	0	0	3	0	0	0	0	1	1	0	3	0	0	0	0	3	1	0	0	3	0	1	0	3	3	0	0	0	0	0	0	0	0	0	0	2	3	0	0	0	3	0	0	3	0	0
Limnebius	0	3	0	0	0	0	0	1	3	0	3	1	3	0	0	2	0	0	0	0	0	0	3	0	2	1	0	3	0	0	0	0	3	0	0	2	3	0	1	0	3	3	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	1	3	0	0	0	0
Limnephilus	0	0	0	3	2	0	0	3	0	0	3	0	3	3	3	0	0	0	0	3	0	0	1	0	0	1	0	2	2	0	0	0	2	2	2	0	0	0	0	0	0	5	0	0	0	0	0	1	5	0	2	1	0	0	0	0	0	3	0	0	0	0	0
Limnius	0	3	0	0	0	0	0	1	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	0	1	0	0	4	0	1	0	0	0	1	0	3	0	0	0	0	0	0	0	1	3	0	0	0	0
Lymnaea	0	0	0	0	3	3	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	0	1	0	3	0	0	0	0	0	1	2	3	0	3	0	2	0	0	0	1	3	0	0	2	0
Meladema	0	0	0	0	3	0	0	0	3	0	3	0	3	3	0	2	0	0	0	3	0	0	0	0	1	1	0	3	0	0	0	0	3	1	0	0	3	0	1	0	3	3	0	0	0	0	0	0	0	0	0	0	1	3	1	0	0	3	0	0	3	0	0
Micronecta	3	1	0	0	0	0	0	3	0	0	0	2	3	3	0	3	0	0	3	2	0	0	0	0	3	1	0	0	0	0	0	1	0	1	0	1	1	0	0	0	3	2	0	0	0	0	0	0	0	2	2	0	3	0	0	0	0	3	2	0	3	0	0
Mystacides	0	0	3	1	0	0	0	3	0	0	3	0	3	3	3	0	0	0	0	3	0	0	0	0	1	1	1	2	0	0	0	0	3	3	1	0	0	0	0	0	1	4	0	0	0	0	0	2	0	2	4	0	0	1	0	0	1	3	2	0	0	0	0
Naucoris	0	0	0	3	0	0	0	3	0	0	1	1	2	3	0	2	0	0	1	0	0	3	0	0	1	3	0	2	0	0	0	1	0	0	0	0	3	0	1	2	3	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	3	1	0
Nemoura	0	1	3	0	0	0	0	2	2	2	2	0	3	3	0	0	0	0	3	1	0	0	0	0	2	2	0	2	0	0	0	1	3	3	0	0	0	0	0	0	0	5	0	0	0	0	0	1	2	1	0	0	0	0	0	0	0	3	0	0	0	0	0
Notonecta	0	0	0	3	0	0	0	3	2	0	3	0	3	3	0	2	0	0	0	1	0	3	0	0	0	2	0	3	1	0	0	3	0	1	0	1	3	0	2	2	4	0	0	0	0	0	0	0	0	0	0	0	3	3	1	0	0	0	0	0	3	1	0
Odontocerum	0	0	0	3	1	0	0	3	2	2	3	0	3	3	3	0	0	0	0	0	0	0	3	0	3	1	1	2	0	0	0	0	3	2	3	0	0	0	0	0	0	3	2	0	0	0	0	0	0	1	3	0	3	2	0	0	0	3	0	0	0	3	0
Onychogomphus	0	0	0	0	3	0	0	0	3	3	1	0	3	3	0	0	0	1	3	0	0	0	0	0	2	1	0	3	3	0	0	0	0	1	3	0	0	0	0	0	0	2	3	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	3	0
Orthetrum	0	0	0	1	3	0	0	0	3	3	0	0	3	3	0	0	0	1	2	0	0	0	0	0	1	1	0	3	0	0	0	2	0	1	3	0	0	0	0	0	1	3	1	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	3	0
Oulimnius	0	3	0	0	0	0	0	1	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	0	1	0	0	4	0	1	0	0	0	1	0	3	0	0	0	0	0	0	0	1	3	0	0	0	0
Peltodytes	0	3	0	0	0	0	0	1	3	0	1	3	3	3	0	2	0	0	0	3	0	0	0	0	0	1	0	3	0	0	0	0	3	2	3	0	3	0	1	0	3	3	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	3	0	0
Philopotamus	0	0	1	3	0	0	0	3	0	0	3	0	3	3	3	0	0	0	0	3	0	0	0	0	1	1	1	1	0	0	0	2	2	3	0	0	0	0	0	0	0	2	0	0	3	0	0	2	0	3	1	0	0	1	0	0	0	0	2	3	0	1	0
Physa	0	0	1	3	0	0	0	3	1	0	3	0	3	0	0	3	0	0	0	3	0	0	0	0	2	1	0	0	0	0	0	1	1	3	1	0	0	0	0	2	0	4	0	0	0	0	0	0	3	5	1	1	0	1	0	0	0	1	3	0	0	0	0
Platycnemis	0	0	0	3	0	0	0	0	2	2	3	0	3	3	0	0	0	0	0	0	0	3	0	0	1	1	0	3	0	0	0	2	2	1	3	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	0	3	0
Polycentropus	0	0	1	3	0	0	0	3	1	1	3	2	3	3	3	0	0	0	0	3	0	0	0	0	1	1	1	2	0	0	0	1	3	3	0	0	0	0	0	0	1	1	0	0	3	0	0	1	1	3	1	0	3	4	0	0	0	1	0	1	0	3	0
Pyrrhosoma	0	0	0	3	0	0	0	3	2	2	2	1	3	3	0	0	0	0	0	0	0	3	0	0	2	1	0	3	0	0	0	0	3	1	3	0	0	0	0	0	1	4	0	0	0	0	0	0	0	0	0	0	1	4	0	0	0	0	0	0	0	3	0
Radix	0	0	0	1	3	0	0	2	3	0	3	0	3	0	0	3	0	0	0	3	0	0	0	0	2	1	0	0	0	0	0	2	0	3	0	0	0	0	0	1	0	3	0	0	0	0	0	0	3	5	3	1	3	1	0	0	0	1	3	0	0	0	0
Riolus	0	3	0	0	0	0	0	1	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	0	1	0	0	4	0	1	0	0	0	1	0	3	0	0	0	0	0	0	0	1	3	0	0	0	0
Sialis	0	0	0	3	2	0	0	0	3	3	1	0	0	3	0	0	0	0	0	3	0	0	3	0	0	2	0	1	0	0	0	0	0	0	3	0	1	0	0	0	1	4	3	0	0	0	0	1	1	0	0	1	1	5	0	0	0	0	0	0	0	3	0
Sphaerium	0	0	0	3	1	0	0	1	3	0	3	3	3	3	0	3	3	0	0	0	0	0	0	0	2	1	1	0	0	0	0	1	0	1	3	0	0	0	0	0	0	1	4	0	2	0	0	3	0	5	1	0	2	0	0	0	0	0	0	3	0	0	0
Stactobia	3	1	0	0	0	0	0	3	0	0	0	3	3	3	3	0	0	0	0	3	0	0	0	0	1	1	2	1	0	0	0	0	3	3	0	0	0	0	0	0	0	5	0	0	0	0	0	1	0	1	3	0	0	0	0	0	0	0	0	0	3	0	0
Stictonectes	0	3	0	0	0	0	0	1	3	0	1	3	3	3	0	2	0	0	0	3	0	0	0	0	1	1	0	3	0	0	0	0	3	1	0	0	3	0	1	0	3	3	0	0	0	0	0	0	0	0	0	0	2	3	0	0	0	3	0	0	3	0	0
Sympetrum	0	0	0	3	0	0	0	3	0	0	3	1	2	3	0	0	0	3	0	0	0	0	1	0	1	0	0	3	2	0	0	0	3	1	3	0	0	0	0	0	2	4	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	3	0
Tinodes	0	1	3	1	0	0	0	3	0	0	2	3	3	3	3	0	0	0	0	3	0	0	0	0	2	1	1	1	0	0	0	0	3	3	0	0	0	0	0	0	0	2	0	0	3	1	0	2	0	3	1	0	2	1	0	0	1	0	3	2	0	1	0
Velia	0	0	3	0	0	0	0	3	0	0	3	1	0	2	0	2	0	0	0	3	0	0	3	0	1	3	0	1	0	0	0	3	0	0	0	0	3	0	1	4	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0	0	0	0	0	0	3	1	0

Appendix 4. Correlogram between canopy cover (CC), the 7 seven sections of "*Índice de Hábitat Fluvial*" (IHF) (i.e., the substrate inclusion in riffles and sedimentation in pools, B1; the frequency of riffles, B2; the substrate diversity, B3; the flow velocity and depth regime, B4; the shade percentage in the channel, B5; the habitat heterogeneity elements, B6; the aquatic vegetation coverage, B7; Pardo *et al.*, 2004) and its global score and hydrological isolation (i.e., low flow permanence). Positive correlations were displayed in blue and negative correlations in red colour. Colour intensity was proportional to the correlation coefficients.



	CC	B1	B2	B3	B4	B5	B6	B7	IHF	Flow permanence
CC	1	-0.34	0.63	0.26	0.46	0.89	0.72	0.41	0.72	0.59
B1	-0.34	1	-0.26	-0.12	-0.01	-0.15	-0.41	-0.29	-0.14	-0.54
B2	0.63	-0.26	1	0.37	0.77	0.69	0.8	0.36	0.83	0.74
B3	0.26	-0.12	0.37	1	0.27	0.41	0.35	0	0.51	0.18
B4	0.46	-0.01	0.77	0.27	1	0.55	0.59	0.18	0.7	0.6
B5	0.89	-0.15	0.69	0.41	0.55	1	0.72	0.18	0.73	0.56
B6	0.72	-0.41	0.8	0.35	0.59	0.72	1	0.48	0.83	0.67
B7	0.41	-0.29	0.36	0	0.18	0.18	0.48	1	0.65	0.38
IHF	0.72	-0.14	0.83	0.51	0.7	0.73	0.83	0.65	1	0.61
Flow permanence	0.59	-0.54	0.74	0.18	0.6	0.56	0.67	0.38	0.61	1

Appendix 5a: Plots showing the responses of taxonomic and functional metrics to spatial isolation (surrounding water): (a) taxonomic richness; (b) % richness of Chironomidae taxa; (c) % richness other Diptera; (d) EPT (Ephemeroptera, Plecoptera and Trichoptera) richness; (e) OCH (Odonata, Coleoptera and Hemiptera) richness; (f) functional richness; (g) functional redundancy; (h) functional dispersion and (i) mean functional similarity between taxa. Solid lines represent the fitted values of generalized linear models (see Table 2).



Appendix 5b: Plots showing the responses of dispersal traits to spatial isolation (surrounding water): (a) % aerial active; (b) % aerial passive; (c) % aquatic active and (d) % aquatic passive dispersal. Solid lines represent the fitted values of generalized linear models (see Table 2).