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Navigating through space and time: A methodological approach to quantify spatiotemporal connectivity using stream flow data as a case study

David Cunillera-Montcusí[1,2,3,4] | José María Fernández-Calero[1,2] | Sebastian Pölsterl[5] | Roger Argelich[1] | Pau Fortuño[1,2] | Núria Cid[1,6] | Núria Bonada[1,2] | Miguel Cañedo-Argüelles[1,7,8]

[1]FEHM-Lab (Freshwater Ecology, Hydrology and Management), Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona (UB), Diagonal 643, 08028, Barcelona, Spain; [2]Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona (UB), Diagonal 643, 08028, Barcelona, Spain; [3]Departamento de Ecología y Gestión Ambiental, Centro Universitario Regional del Este (CURE), Universidad de la República, Tacuarembó s/n, Maldonado, Uruguay; [4]GRECO, Institute of Aquatic Ecology, University of Girona, Girona, Spain; [5]The Lab for Artificial Intelligence in Medical Imaging (AI-Med), Department of Child and Adolescent Psychiatry, Ludwig-Maximilians-Universität, Nussbaumstraße 5, 80336, Munich, Germany; [6]IRTA Marine and Continental Waters Programme, Ctra de Poble Nou Km 5.5, E43540, La Ràpita, Catalonia, Spain; [7]Institut de Recerca de l'Aigua (IdRA), Universitat de Barcelona (UB), Diagonal 643, 08028, Barcelona, Catalonia, Spain and [8]Institute of Environmental Assessment and Water Research (IDAEA-CSIC), Carrer de Jordi Girona, 18-26, 08034, Barcelona, Spain

Correspondence
David Cunillera-Montcusí
Email: david.cunillera@dcm.cat

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Abstract

1. The growing interest in combining spatial and temporal patterns in nature has been fostered by the current availability of high-frequency measurements. However, we still lack a methodological framework to process and interpret spatiotemporal data-sets into meaningful values, adaptable to different time windows and/or responding to different spatial structures. Here, we developed and tested a framework to evaluate spatiotemporal connectivity using two new measures: the spatiotemporal connectivity (*STcon*) and the spatiotemporal connectivity matrix (*STconmat*).

2. To obtain these measures, we consider a set of spatially connected sites within a temporally dynamic network. These measures are calculated from a spatiotemporal matrix where spatial and temporal connections across sites are captured. These connections respond to a determined network structure, assign different values to these connections and generate different scenarios from which we obtain the spatiotemporal connectivity. We developed these measures by using a dataset of stream flow state spanning a 513-day period obtained from data loggers installed in seven temporary streams. These measures allowed us to characterise connectivity among stream reaches and relate spatiotemporal patterns with macroinvertebrate community structure and composition.

3. Spatiotemporal connectivity differed within and among streams, with *STcon* and *STconmat* capturing different hydrological patterns. Macroinvertebrate richness and diversity were higher in more spatiotemporally connected sites.

Community dissimilarity was related to *STconmat* showing that more spatiotemporally connected sites had similar communities for active and passive dispersers. Interestingly, both groups were related to spatiotemporal connectivity patterns for some of the analysed scenarios, highlighting the relevance of spatiotemporal connectivity in dynamic systems.

4. As we exemplified, the proposed framework can help to disentangle and quantify spatiotemporal dynamics or be applied in the conservation of dynamic systems such as temporary streams. However, the current framework is not limited to the temporal and spatial features of temporary streams. It can be extended to other ecosystems by including different time windows and/or consider different network structures to assess spatiotemporal patterns. Such spatiotemporal measures are especially relevant in a context of global change, with the spatiotemporal dynamics of ecosystems being heavily disrupted by human activities.

1 | INTRODUCTION

The interaction between populations, communities and ecosystems within a landscape has a prominent role in ecology (Gounand et al., 2020; Hanski, 1999; McArthur & Wilson, 1967). To better understand this interaction, the so-called meta-system framework has been developed (Cid et al., 2022; Gounand et al., 2018; Schiesari et al., 2019). This framework asserts that landscape connectivity drives exchanges of matter, energy and organisms among localities within a landscape, affecting ecosystem structure, functioning and dynamics (Battin et al., 2009; Dale, 2017; Larsen et al., 2012). For example, several studies have highlighted the relevance of connectivity in driving species' diversity and abundance (Borthagaray et al., 2020; Economo & Keitt, 2010), community turnover (Epele et al., 2021; Horváth et al., 2016), population synchrony (Larsen et al., 2021; Sarremejane et al., 2021), mutualistic interactions (Ferreira et al., 2020; Monteiro et al., 2022), species' extinctions (Horváth et al., 2019), vulnerability to species invasions (Drake et al., 2017) and ecosystem services (Mitchell et al., 2013). Therefore, connectivity is emerging as one of the main drivers of community assembly and ecosystem functioning as it varies the strength of dispersal (Leibold & Chase, 2018; Thompson et al., 2020; Vellend, 2016) and affects biodiversity, which is linked to ecosystem properties such as resistance or productivity (Thompson et al., 2017; Tonkin, Heino, et al., 2018). Nevertheless, most of these examples are focused on spatial connectivity, while the temporal facet of connectivity remains relatively understudied (Uroy et al., 2021).

Metapopulations, metacommunities and meta-ecosystems have been generally assessed using a snapshot approach that assumes temporal stability (Holyoak et al., 2020; Uroy et al., 2021). In the specific case of metacommunities, most studies have considered spatial or temporal connectivity individually while communities experience both temporal and spatial variation in connectivity affecting populations (Kurihara, 2007), communities (Cañedo-Argüelles et al., 2020; Dong et al., 2017) and ecological processes (Ding et al., 2013; Sadchatheeswaran et al., 2021). Whereas spatial connectivity refers to how communities are connected within a landscape (Moritz et al., 2013), temporal connectivity refers to how communities are connected in time, for example, across multiple years (Holyoak et al., 2020). Within this context, considering only one facet of connectivity can lead to misleading conclusions about the importance of landscape connectivity for the exchange of species between local communities (Castillo-Escrivà et al., 2020; Huang et al., 2020; Rasmussen et al., 2013). To date, few studies have assessed how connectivity changes simultaneously in space and time, defined here as spatiotemporal connectivity, and how these can affect natural systems (Fullerton et al., 2010; Uroy et al., 2021).

Nowadays, new technologies such as satellite high-frequency sensors (Burel & Baudry, 2005; Ducklow et al., 2009; Pekel et al., 2016), high time frequency measuring devices such as GPS (Bischof et al., 2019; Fattebert et al., 2015; Foley & Sillero-Zubiri, 2020) or data loggers (Crabot et al., 2020; Jensen et al., 2019; Vander Vorste et al., 2016) offer good opportunities to characterise spatiotemporal connectivity because they capture high spatial and temporal resolution data that can be later combined into spatiotemporal measures (Martensen et al., 2017; Uroy et al., 2021). Some studies have used long-term datasets to assess the temporal variation of spatial processes through consecutive snapshot analyses (Cañedo-Argüelles et al., 2020; Leppänen et al., 2019; Rouissi et al., 2014), but in these studies, the interaction between different time steps is not considered. In contrast, other studies (Huang et al., 2020; Martensen et al., 2017; Thompson et al., 2017) simultaneously consider the interaction between spatial and temporal dimensions by including the effect of connectivity through more

than one time step (e.g. the connectivity of a given time point has an effect on the next time points and this effect propagates in time). However, few examples exist where spatial and temporal variation are simultaneously considered to estimate spatiotemporal connectivity (Uroy et al., 2021). The lack of a clear framework from which to calculate spatiotemporal connectivity values or assess different time windows (i.e. number of time steps considered to impact connectivity) is limiting the development of such approximations. Even though technologies to capture spatiotemporal connectivity changes are nowadays available, we still need a methodological framework for obtaining connectivity measures that integrate spatial and temporal patterns (Uroy et al., 2021).

Temporary river networks are suitable systems to analyse and develop a framework to assess spatiotemporal connectivity due to their high hydrological variability in space and time (Datry et al., 2014). Spatially, fluvial systems are driven by an up- to downstream unidirectional flow following a dendritic structure which affects the distribution and presence of species (Altermatt, 2013; Altermatt et al., 2020; Borthagaray et al., 2020; Schmera et al., 2018). Temporally, they are subjected to a strong seasonal and/or interannual variation, with recurrent drying and flowing periods determining habitat availability (Bonada et al., 2020; Datry et al., 2016; Valente-Neto et al., 2020). Finally, species inhabiting these systems have two different strategies to withstand drying and thus coping with spatiotemporal variability: resisting in situ as dormant stage (temporal dispersal) or recolonising from nearby refuges after flow resumption (spatial dispersal; He et al., 2020; Heino, 2013; Sarremejane et al., 2020). These different ways of interacting with the landscape can be related to different network structures or dispersal abilities, thereby informing about changes in network connectivity (Cañedo-Argüelles et al., 2020; Pineda-Morante et al., 2022; Tonkin, Altermatt, et al., 2018). Consequently, in temporary streams, spatiotemporal connectivity among communities is promoted by unidirectional or by multidirectional dispersal (Borthagaray et al., 2015; Seymour et al., 2015; Tonkin, Altermatt, et al., 2018). A unidirectional or directed network would be related to species that are aquatic obligates and that follow the stream dendritic structure to move from one site to another, hereafter passive dispersers. A multidirectional or undirected network would be related to species that can fly in all directions, with no need to follow the stream course, hereafter aerial dispersers. So far, flow data obtained using high-frequency temperature data loggers have been used to characterise the local hydrological conditions of temporary streams (e.g. drying duration, number of consecutive dry days, days with disconnected pools, days after flow return) and its effects on aquatic communities (Arias-Real et al., 2021; B-Béres et al., 2019; Beesley & Prince, 2010; Crabot et al., 2020). However, this information has not yet been used to develop spatiotemporal connectivity measures.

In this study, we developed a methodological framework to assess spatiotemporal connectivity focusing on Mediterranean streams as a case study. Using high-frequency data on water presence/absence from a set of temporary streams, we propose two measures of connectivity (Figure 1): spatiotemporal connectivity (*STcon*) and spatiotemporal connectivity matrix (*STconmat*). *STcon* measures average
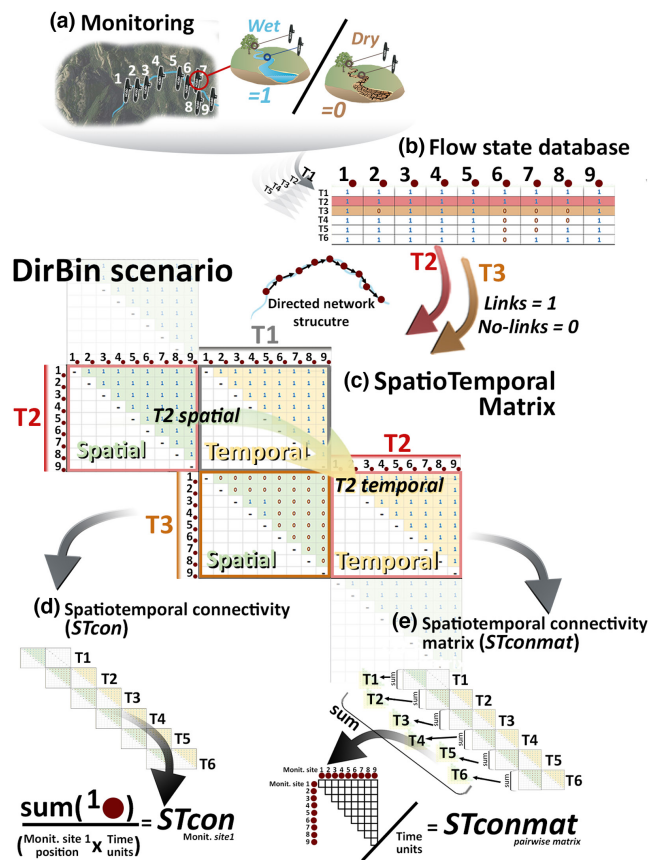
FIGURE 1 Conceptual graphical representation of how the *STcon* and *STconmat* are calculated using the example of Vall d'Horta stream (VH). (a) The data loggers are deployed in the field and monitor the presence (i.e. wet) or absence (i.e. dry) of water. (b) These values are then presented in a flow state database where rows represent each time unit (i.e. 6 days, from T1 to T6) and columns every monitored site (from 1 to 9). Each cell of the flow state database is filled with a value of '1' if the monitored site was 'wet' that day (e.g. all sites in day 1, T2, were defined as 1) or with a value of '0' if the monitored site was 'dry' that day (e.g. in day 2, T3, monitored site 2, 6, 7 and 8 were defined as 0). (c) Using the flow state database, the spatiotemporal matrix is built based on a defined scenario, in this case, we used a directed network structure and a binary quantification of links and no-links (DirBin scenario). For each row of the flow state matrix (e.g. T2), a pairwise matrix is constructed where all the possible spatial links, based on which monitored sites are 'wet' and which are 'dry', are assessed. This defines the spatial connections for a specific time (green part of the matrix). Temporal connections are filled based on the same connections of that time (T2) but introduced in the spatiotemporal matrix in the following time step (T3). (d) *STcon* is calculated for each site individually (e.g. Site 1) and is the average of how often a site has been connected to all its potential neighbours (e.g. Site 1 has eight potential neighbours) during the studied time (6 units of time). (d) *STconmat* corresponds to the sum of all the spatiotemporal matrices into one unique matrix later divided by the studied time (6 units of time).

site connectivity for each individual site and thus can be used as a predictor of community structural and functional metrics such as local species richness or Shannon–Wiener diversity. *STconmat* represents

these connectivity values by pairs of sites so as a spatiotemporal connectivity matrix and allows to assess changes in community composition (e.g. Jaccard dissimilarity, Bray–Curtis dissimilarity). Here, we used these two measures to explain changes in the structure of macroinvertebrate communities at the local and regional scales to illustrate their relevance for capturing ecological processes.

2 | MATERIALS AND METHODS

2.1 | Study sites and sampling

The dataset used for developing and testing the current framework comes from a study carried out in Sant Llorenç del Munt i l'Obac Natural Park, a protected area in the Vallès Occidental region (Catalonia, NE Spain). The area has a Mediterranean climate and the underlying geology is dominated by karst limestone. These characteristics make surface flows heavily linked to rainfall events and thus streams in the region have marked flowing/drying periods, especially during the summer. We selected seven temporary streams that were sampled in November 2019 as part of a yearly seasonal monitoring where streams were monitored from July 2018 until November 2019. All streams had similar instream characteristics and aquatic macroinvertebrates were sampled following a multihabitat design and identified at the lowest possible taxonomic level, mostly species or genus. Information on sampling location, procedure, characteristics and specific taxonomic identification can be found in Pineda-Morante et al. (2022).

2.2 | Flow state monitoring and database building

A total of 69 temperature data loggers (HOBO Pendant® Temperature/Light logger, hereafter loggers) were used to assess flow state in the seven selected streams (Figure 1a), with between 10 and 15 loggers per stream (Figure S1; Pineda-Morante et al., 2022). These data loggers were installed in July 2018 and kept in the streams until December 2019. At each study site, a logger was submersed into the water to record water temperature (°C) and, for each stream, a logger was placed outside the water (e.g. hanging from a tree) to record air temperature (°C). The loggers recorded temperature at hourly intervals for 513 days. We calculated the daily mean temperature and compared the diurnal temperature variation of the installed loggers to assess if each site had enough water to cover the data logger (hereafter wet) or no surface water (hereafter dry) comparing air and instream temperatures following Gungle (2006). Those estimations were validated using field observations and time-lapse images taken for some streams. Finally, we used a logistic regression model including stream characteristics to correct the missing values generated due to loggers malfunctioning or loss due to climatic events (e.g. temperatures below 0°C, floods). Specific details about the model and the process of predicting missing data can be found in Pineda-Morante et al. (2022). The final dataset resulted in a table with the daily wet/dry values (rows) for each logger (columns) for each one of the monitored streams. In this table, a wet day with the presence of surface water flowing or as disconnected pools is represented by '1' and a dry day by '0'. This dataset constitutes the basic information from which we later calculated all the spatiotemporal indices. In this work, we used the entire 513-day period to calculate all the spatiotemporal indices. Using the same flow state database obtained with the data loggers, we also calculated several local hydrological metrics commonly used to characterise surface flow state in temporary streams (Arias-Real et al., 2021; Crabot et al., 2020; Pineda-Morante et al., 2022), such as the total number of dry days (TotDur), the number of changes from wet to dry days (TotNum) and the average number of dry days for each drying event (TotLeng).

2.3 | Building spatiotemporal matrices based on logger data

Spatiotemporal connectivity was obtained after building a spatiotemporal matrix, hereafter ST matrix, for each stream. Each row and column of the ST matrix corresponded to a monitored site with a data logger deployed at a specific time (Figure 1b). Therefore, the matrix was as big as many sites and times were monitored. Then, the ST matrix was filled with information regarding the two levels of connectivity that we assessed: spatial and temporal.

2.3.1 | Spatial connection

Spatial connections were built based on a defined stream network structure (Figure 1c). A directed structure follows an upstream–downstream direction (Figure S2) and an undirected structure implies that all nodes can be reached from everywhere (Figure S2). This structure was related to the dispersal modes of the organisms that we wanted to study. We assumed that passive dispersers would disperse mostly downstream by drift so they would mainly respond to a directed network. Contrarily, active dispersers that disperse by flight would mostly respond to an undirected network. In the two networks used to create the ST matrix, each node represented a monitored site and each link an effective connection between sites. If the node's flow state was considered as wet, the connection with other nodes was possible. Following the paths defined by the network, the number of reachable nodes from each monitored site was assessed (Figure 1c; Spatial). In the case that a monitored site was dry for that day, the connection with this dry site or throughout it was not possible.

2.3.2 | Temporal connections

Temporal connections were built in the same way as spatial links (Figure 1c; Temporal). All the possible connections within the network for a specific time were assessed based on the same network structure of the spatial ones. However, the temporal links were entered in the ST matrix on the following time step. In other words, we

considered that the connection between the nodes on a given day would influence their connectivity on the following day (Figure 1c; T2 Temporal connections).

2.3.3 | Link and no-link values

For each node, all the spatial and temporal connections with its neighbours were filled with the values corresponding to what we defined as the *link* or *no-link* value (Figure 1c). The *link* value is the value that we give when dispersal can occur between two nodes. In this study, this occurs when the flow state is 1 in a pair of nodes and the path to reach them. Contrarily, the n*o-link* value is the value given when dispersal is not possible or in our case, there is at least one 0 in the path between a given pair of nodes. *Link* and *No-link* values can be modified depending on how connected and unconnected sites are defined. These values can be modified in the function *spat_temp_index*, an R function created to calculate the spatiotemporal connectivity metrics (Cunillera-Montcusí, 2023), to define different scenarios. Therefore, the current framework allows for calibrating spatiotemporal connections between sites and can include any ecologically meaningful network structure or link interpretation (Cañedo-Argüelles et al., 2015; Phillipsen & Lytle, 2013).

2.3.4 | Binary and weighted scenarios

In this study, we designed four different scenarios from which we calculated *STcon* and *STconmat* to exemplify different possibilities of the current framework. Each scenario combined a different network structure, directed or undirected, and a different way of quantifying the *links* and *no-links* (binary and weighted). For the two **binary scenarios**, the directed binary (hereafter DirBin) and the undirected binary (hereafter UndBin), the *link* value was defined as 1 and the *no-link* value as 0. Therefore, *STcon* and *STconmat* were quantifying the number of times that each site was connected to its neighbours. For these scenarios, high values meant that a site was highly connected to its potential neighbours during the considered time.

For the other two **weighted scenarios**, the directed weighted (DirWei) and the undirected weighted (UndWei), we added an additional variable: the Euclidean distance between sites. Here, the *link* value was 0.1 and the *no-link* value was 1, and these values were multiplied by the distance between the two nodes. Thus, for the weighted scenarios, we assumed that the presence of water between two sites was facilitating dispersal. Consequently, when connection was possible, the Euclidean distance between two sites was reduced by 90% and when connection was not possible, the Euclidean distance between these two sites was preserved. Therefore, *STcon* and *STconmat* calculated for the DirWei and UndWei scenarios were assessing dispersal resistance. For these scenarios, high and low resistance values indicate that the connectivity between two sites is low and high respectively.

2.4 | Spatiotemporal connectivity measures

Once the ST matrix was filled with the corresponding *link* and *no-link* values, *STcon* and *STconmat* were calculated. Depending on the desired output, connectivity can be either calculated for each site individually resulting on the *STcon* measure, or as a pairwise matrix that incorporates the relation of each site with all the other pairs within the network, resulting in the *STconmat*.

The *STcon* corresponds to the average of all the spatial and temporal links for each individual node (Figure 1d). To calculate it, we summed all the times that a node had been connected to its neighbours both spatially and temporally, and later, we divided that value by the amount of time considered and the total potential neighbours that the individual node can have: $STcon = \sum_{Tx}(S_i + T_i)/Nneigh_i \times TTU$. Where $\sum_{Tx}$ is the sum of values through all considered times, S_i and T_i are the spatial and temporal connections of a specific node i with its neighbours, $Nneigh$ corresponds to all the potential neighbours that node i has and TTU is the total time units considered. Therefore, *STcon* represents an average value of how often an individual node has been connected to all their potential neighbours (Figure 1c). In the case of a directed network structure, the value is calculated considering each site's outflow path, which identifies the relevance of each site as a source of colonists for all their neighbours. As *STcon* is averaged by the total potential neighbours of each site, *STcon* can be compared within sites of the same system and among systems. For the *STconmat*, we summed the ST matrix in a unique pairwise matrix including all stream sites (Figure 1e). We then divided this pairwise matrix by the amount of time considered being $STconmat = [(S(i_1 - n_1)...n) + (T(i_1 - n_1)\cdots n)]/TTU$, where S and T are the spatial and temporal links for each pair of nodes, and TTU the total time units considered. Therefore, *STconmat* is averaging daily spatial and temporal connections for each pair of nodes. Both *STcon* and *STconmat* capture the spatiotemporal connectivity of each site during the studied period and their values are directly related to the values assigned to *link* and *no-link*.

2.5 | Testing the spatiotemporal connectivity measures

For each one of the four scenarios, DirBin, DirWei, UndBin and UndWei, we calculated *STcon* and *STconmat* for the entire monitored period of 513 days. We conducted a principal components analysis, PCA, including the *STcon* values for each scenario and the three local hydrological variables (TotNum, TotDur and TotLeng) to analyse how they were correlated based on the Euclidean distances between them, using *prcomp* function from STATS package (R-Core Team, 2019). We used the *adonis* function from VEGAN (Oksanen et al., 2010) to test if upstream–downstream position or stream ID were presenting similar values in this multivariate space using a permutational analysis of variance (PERMANOVA) and expecting that the high hydrological variability in the sampled streams would result in significant differences among them. In addition, we used

Spearman correlations for the same set of variables to test their correlation and quantify the strength of their relationship.

As *STcon* and *STconmat* differ in their structure, the approach to characterise each stream was also different. First, we related *STcon* to the relative position of each monitored site within each stream network in an up- to downstream direction. Second, we analysed the differences in *STconmat* for each stream in a multivariate space through a non-metric multidimensional scaling (NMDS). As *STconmat* is a pairwise matrix, the values are equivalent to spatiotemporal distances between sites and can be represented in a bidimensional space.

Finally, to test *STcon* and *STconmat* against macroinvertebrate community's metrics, we used the period of 480 days between the start of the monitoring (26/07/2018) until the biological sampling campaign (18–21/11/2019) to build the spatiotemporal connectivity metrics. We considered this period for the four different scenarios (DirBin, DirWei, UndBin and UndWei). As the two network structures were related to different dispersal abilities (i.e. directed for aquatic passive and undirected for aerial active), we split the community matrix in these two dispersal groups based on available biological trait data (Pineda-Morante et al., 2022; Sarremejane et al., 2020; Tachet et al., 2010). We did not account for aquatic active and aerial passive dispersers because of their low abundance representing both around 12% of sample's total abundance. For both aquatic passive and aerial active dispersers, we calculated taxonomic richness, Shannon–Wiener diversity, relative dispersal traits abundance and compared them against STcon. We also calculated two beta diversity proxies: Jaccard, based on presence–absence, and Bray–Curtis, based on abundance data and compared them against STconmat. These metrics were calculated using the VEGAN package (Oksanen et al., 2010). Finally, linear mixed models were used to analyse the relationship between *STcon* and the calculated community metrics (taxonomic richness, Shannon–Wiener diversity, relative dispersal traits abundance) using the package LME4 (Wood & Scheipl, 2013) and considering stream identity as a random factor to control for variability between the different streams. We analysed all pairwise distance matrices with Mantel tests relating *STconmat* to the two community dissimilarity metrics (Bray–Curtis and Jaccard indices) using the VEGAN package (Oksanen et al., 2010).

3 | RESULTS

3.1 | Spatiotemporal connectivity and network structure

The selected streams showed strong differences in their spatiotemporal patterns in relation to network structure. In the binary scenarios DirBin and UndBin, where direct connectivity is quantified, both *STcon* (Figure 2a) and *STconmat* (Figure 2b) captured wet/dry patterns for each monitored site. For example, sites that dry more often and for longer durations had lower values of *STcon* for the DirBin and UndBin scenarios (Figure 2; site highlighted in red). When

the network structure was directed (DirBin), the sites that were dry more often were impacting other sites located above them by reducing their *STcon* and *STconmat* values as these sites cannot connect to their downstream neighbours when an intermediate site is dry (Figure 2; DirBin, sites above the one highlighted in red). On the contrary, this effect was not observed for the undirected network structure (Figure 2; UndBin). In the weighted scenarios DirWei and UndWei (Figure 2), where *STcon* and *STconmat* quantified dispersal resistance, the highest values were found at upstream sites when there was a directed structure, DirWei, whereas the drier sites had the greatest values of *STcon* and *STconmat* in the undirected network UndWei (Figure 2; site highlighted in red). In weighted scenarios, *STcon* and *STconmat* captured the interaction between distance and drying so when a site contained water the distance between two sites decreased concomitantly with *STcon* and *STconmat* values. Contrarily, when a site was dry, the distance corresponded to the Euclidean distance between the sites leading to an increase of *STcon* and *STconmat* values. The complete dataset with *STcon* and *STconmat* values for the four scenarios and for all the monitored streams can be seen in Figure S3 and Table S1.
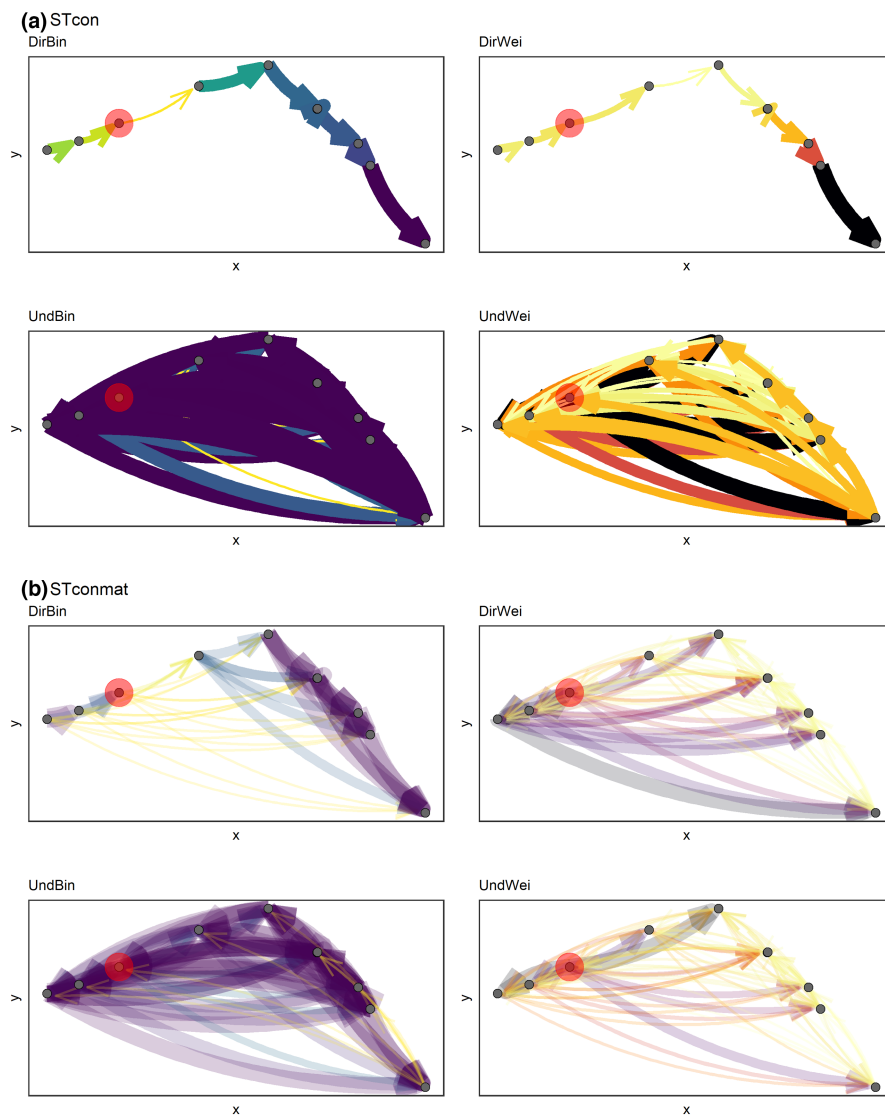
3.2 | Spatiotemporal connectivity and local flow state

When comparing the spatiotemporal indices with previously existing indices based on flow state data (i.e. TotDur, TotNum and TotLeng), we observed that there were negative correlations between the *STcon* and the TotDur (DirBin=−0.69 and UndBin=−0.65) and TotNum (DirBin=−0.51 and UndBin=−0.53) for both directed and undirected networks (Figure 3). Thus, higher values of *STcon* (i.e. high spatiotemporal connectivity) were associated with lower values of TotDur (i.e. total duration of drying events) and TotNum (i.e. frequency of drying events). Spearman correlation analysis highlighted these negative correlations (Figure S4). Finally, for the PERMANOVA analysis, we found significant differences across sites position in the PCA between streams and between site position within streams (i.e. upstream–downstream), and a significant interaction of both factors as expected (Figure 3).

3.3 | Stream spatiotemporal characterisation

STcon differed between streams and between upstream and downstream sections. For the binary non-weighted scenarios (Figure 4a; DirBin and UndBin), there was a general increase in *STcon* towards downstream sites meaning that downstream sites presented higher spatiotemporal connectivity (Figure 4a; DirBin), except for the M and SA streams (where no clear tendency was found). The indices followed an inverse trend in the weighted scenarios as dispersal resistance increased towards upstream reaches (Figure 4a; DirWei and UndWei), especially in the directed scenario (Figure 4a; DirWei). *STcon* captured drier sites impact on connectivity for directed networks (Figure 4a; DirBin and DirWei), which disappeared for

FIGURE 2 (a) *STcon* and (b) *STconmat* values for the Vall d'Horta stream (VH). Colour viridis gradient and size correspond to *STcon* and *STconmat* values. For DirBin and UndBin scenarios, purple/ blue and bigger sized arrows indicate higher connectivity while yellow and smaller arrows indicate isolation. For DirWei and UndWei, grey/red and bigger sized arrows indicate higher dispersal resistance while orange/yellow and smaller arrows indicate less resistance. We highlighted in red the monitored site 3 just to ease its location in the network. All the data are calculated based on the whole monitored time window (513 days). See the other studied streams in Figure S3.

undirected scenarios (Figure 4a; UndBin and UndWei). The NMDS performed using the *STconmat* values (Figure 4b) illustrated the differences in spatiotemporal connectivity between sites within each of the streams. Widely dispersed sites (Figure 4b; VH stream) experienced a higher temporal variation in connectivity than clustered sites (Figure 4b; SC and C streams). STcon values for each individual stream and scenario are available in Figure S5.

3.4 | Testing spatiotemporal connectivity against macroinvertebrates communities

The linear mixed models showed several significant relationships between *STcon* calculated for each of the four scenarios and the three site-specific biodiversity metrics (taxonomic richness, Shannon–Wiener diversity and dispersal traits abundance) for the two dispersal groups (Figure 5a–c). *STcon* was negatively related to the richness of passive dispersers in the DirWei scenario, whereas *STcon* was positively related to the taxonomic richness of both passive and active dispersers in the UndBin scenario. Shannon–Wiener diversity

of passive and active dispersers as well as the dispersal traits abundance of passive dispersers were positively related to *STcon* in the UndBin scenario. We also identified significant relationships between *STconmat* and community dissimilarity (Figure 5d,e). Passive and active dispersers responded significantly to both directed and undirected weighted scenarios, with Bray–Curtis dissimilarity positively related to *STconmat* in the DirWei and UndWei scenarios. Jaccard dissimilarity for passive dispersers was positively related to *STconmat* in the DirBin and UndBin scenarios. Contrastingly, Jaccard dissimilarity for active dispersers was negatively related to *STconmat* in the DirBin scenario. Finally, Jaccard dissimilarity for active dispersers was positively related to *STconmat* in the undirected weighted scenario (UndWei). All community metrics and model effect sizes can be found in Figure S6 and Table S2.

4 | DISCUSSION

We present a new methodological framework from which spatiotemporal connectivity can be calculated combining both spatial
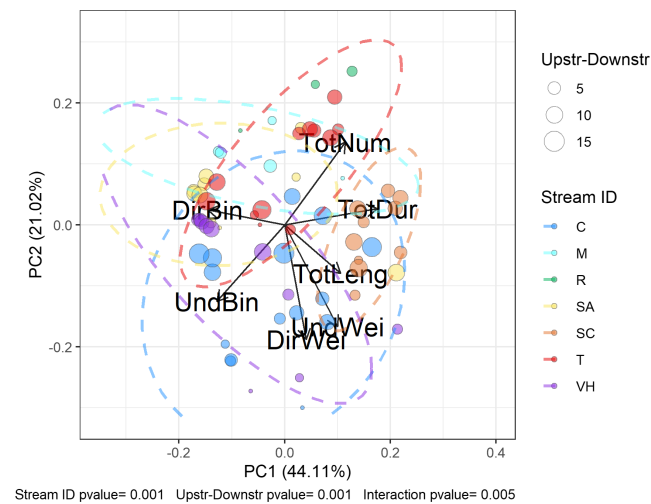
FIGURE 3 PCA plot for *STcon* indices for each one of the four scenarios: directed binary (DirBin), directed weighted (DirWei), undirected binary (UndBin), undirected weighted (UndWei) and the hydrological variables: the total duration of drying events (TotDur), the frequency of drying events (TotNum) and the average length of each drying event (TotLeng). All the data are calculated based on the whole monitored time window (513 days).

and temporal dimensions in one unique value. Our spatiotemporal connectivity measures use data obtained at a continuous time interval (e.g. minutes, days, months, years) and consider a particular spatial structure (i.e. dendritic network or undirected network in our case). We developed this approach using a high-frequency database of flow state where daily wet/dry values of seven streams were recorded for 513 days (Pineda-Morante et al., 2022). Past studies used daily monitoring to assess the spatial variation (i.e. wet or dry reaches) and/or to characterise temporal variation (e.g. seasonal changes) of river networks following a snapshot approach (Crabot et al., 2020; Pineda-Morante et al., 2022). Our framework allows merging spatial and temporal dynamics within the same connectivity value, while being adaptable to different temporal windows, monitoring studies and systems (e.g. months or years with datasets like Mouton et al., 2022; Perera et al., 2020; Ridl et al., 2018). In addition, the framework can incorporate non-binary connections based on, for example, distances, resistance (e.g. non-transitable areas), barriers (e.g. dams, forests) or dispersal pathways (e.g. wind or flow). Therefore, the proposed framework can be extended to any system presenting a spatial structure that has been monitored through time and with enough detail to build a network structure that captures fluxes of individuals, species, energy or matter.

The spatiotemporal connectivity measures developed here captured distinct network connectivity patterns. For example, they showed differences among headwaters and downstream reaches and accounted for how dry reaches acted as dispersal barriers. From a management point of view, such information could prove useful in defining stream typologies according to their spatiotemporal trends and associate different management practices to them (Bonada et al., 2020; Datry et al., 2014; Gallart et al., 2017). For example,

when assessing temporary stream biological quality, one could assign relevance to the terrestrial and/or the aquatic biota according to stream spatiotemporal connectivity patterns (Steward et al., 2022). Furthermore, these spatiotemporal measures can be useful to understand how network connectivity determines the fluxes of energy, matter and organisms within the river (Cid et al., 2022; Gounand et al., 2018; Martensen et al., 2017; Uroy et al., 2021). Although we used high time frequency data loggers to obtain flow state data, the current framework could be applied to data coming from gauging stations (Monk et al., 2008; Stocks et al., 2021; Walker et al., 2016) or from hydrological models (Costigan et al., 2017; Döll & Schmied, 2012; Yu et al., 2020), which could be used to define the values assigned to the 'links' and 'no links' to assess connectivity. In this sense, instead of binary values of connectivity, we could incorporate flow, wind velocity or even permeability values between sites as far as these data would be available at the same temporal resolution. In terms of drying patterns, we found that *STcon* values showed negative correlations with TotNum, TotDur and TotLeng in binary scenarios. These correlations were already expected because both *STcon* and hydrological metrics are quantifying intermittence similarly. For example, high values of *STcon* for the scenario DirBin were negatively correlated with the duration of dry events (TotDur), meaning that highly spatiotemporally connected sites are also the ones which generally have shorter dry events. Nevertheless, these results also suggest that by only using the *STcon*, we would be already capturing drying patterns and the usage of local hydrological metrics such as TotNum, TotDur and TotLeng would not be necessary. Overall, *STcon* and *STconmat* present a great potential to characterise spatiotemporal patterns in streams, representing a powerful tool to guide conservation and restoration actions given the importance of spatiotemporal connectivity for population/community dynamics and ecosystem functioning (Chase et al., 2020; Cid et al., 2020).

Macroinvertebrate communities significantly responded to *STcon*, with different responses for active aerial and passive dispersers, thereby suggesting that our indices captured their dispersal dynamics. Species richness and Shannon diversity increased with greater spatiotemporal connectivity in the UndBin scenario, which seems to quantify the impacts of drying on aquatic communities (Crabot et al., 2020; Pineda-Morante et al., 2022). Furthermore, passive dispersers responded negatively to the DirWei scenario, with the communities experiencing higher resistance to dispersal showing lower richness. Thus, drier and more distant sites had fewer taxa, as seen in other studies (Brooks et al., 2018; Elliott, 2002; Fonseca, 1999; Kappes & Haase, 2012; O'Hop & Wallace, 1983). The differences between active and passive dispersers regarding dispersal resistance highlighted the relevance of overland pathways for active dispersers (Bogan & Boersma, 2012; Cañedo-Argüelles et al., 2015; Phillipsen & Lytle, 2013). Passive dispersers abundance responded positively to *STcon* in the UndBin scenario, indicating that perennial sites would tend to accumulate higher abundances of this dispersal group (Hershkovitz & Gasith, 2013). Interestingly, the fact that passive dispersers appear related to undirected scenarios could be linked to the small distances between sites, which could be overcome during
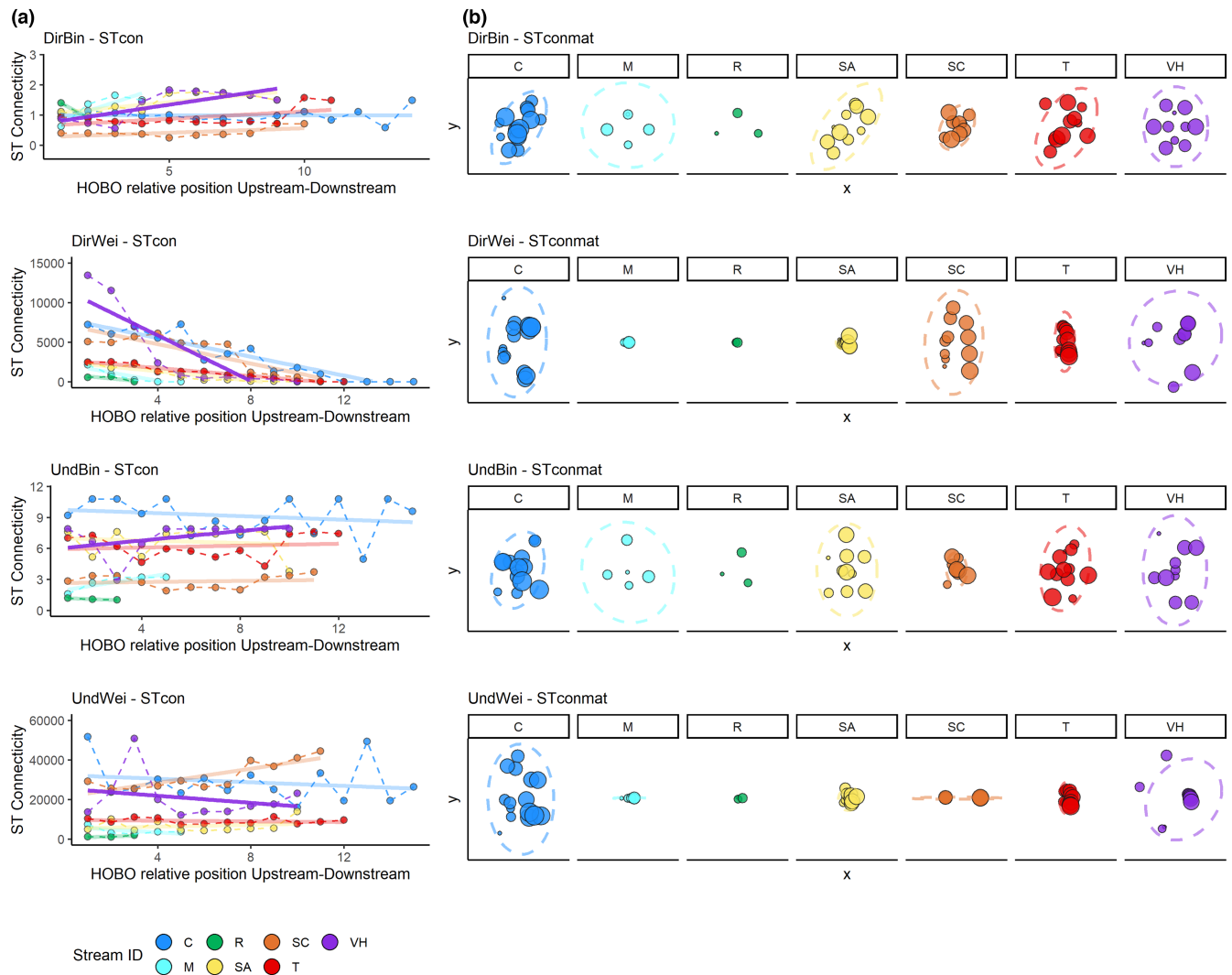
FIGURE 4 (a) Monitored streams *STcon* values (*y*-axis) ordered along their relative position from upstream to downstream (*x*-axis). (b) NMDS with *STconmat* values of each monitored stream. More compact clouds of points mean a greater similarity between sites in terms of spatiotemporal connectivity (i.e. all sites dry similarly). More dispersed clouds indicate a greater variability within the stream in terms of drying. Circle size indicates upstream (smaller) or downstream (bigger) site position. Each plot row corresponds to one of the four scenarios: directed binary (DirBin), directed weighted (DirWei), undirected binary (UndBin), undirected weighted (UndWei). All the data are calculated based on the whole monitored time window (513 days). Individual stream *STcon* plots can be found in Figure S5.

wet conditions (Kappes & Haase, 2012; Razeng et al., 2016) and/or through dispersal vectors such as wind (Cáceres & Soluk, 2002; Epele et al., 2021; Vanschoenwinkel, Gielen, et al., 2008) or animals such as birds and terrestrial mammals (Figuerola & Green, 2002; Frisch et al., 2007; Vanschoenwinkel, Waterkeyn, et al., 2008).

Regarding *STconmat*, both weighted scenarios (DirWei and UndWei) had positive relationships with dissimilarity indices suggesting that dryer and more distant sites harboured more unique communities. Such pattern was probably linked to a combination of dispersal limitation and harsher environmental conditions imposed by drying events leading to higher dispersal resistance and the development of distinct communities (Bonada et al., 2020; Steward et al., 2022; Valente-Neto et al., 2020). On the contrary, the binary scenarios (DriBin and UndBin) resulted in contrasting patterns depending on the dispersal group for presence–absence data. In this

scenario, passive and active dispersers were positively and negatively (respectively) related to spatiotemporal connectivity. This suggests that more connected sites tend to have passive dispersers' communities with different species composition while active dispersers' communities tend to be more similar. Thus, when sites are hydrologically connected for longer periods of time the communities of passive dispersers tend to diverge in their composition. Since many passive dispersers are lost with drying and it takes time for them to recolonise rewetted streams (Bogan & Boersma, 2012; Kappes & Haase, 2012), more perennial sites tend to diverge in their composition as greater species number promotes niche partitioning between habitat patches. In the case of active dispersers, as the spatiotemporal connection between sites increases the communities become more homogeneous due to mass effects (Gansfort et al., 2021; Heino et al., 2015; Sarremejane et al., 2017).
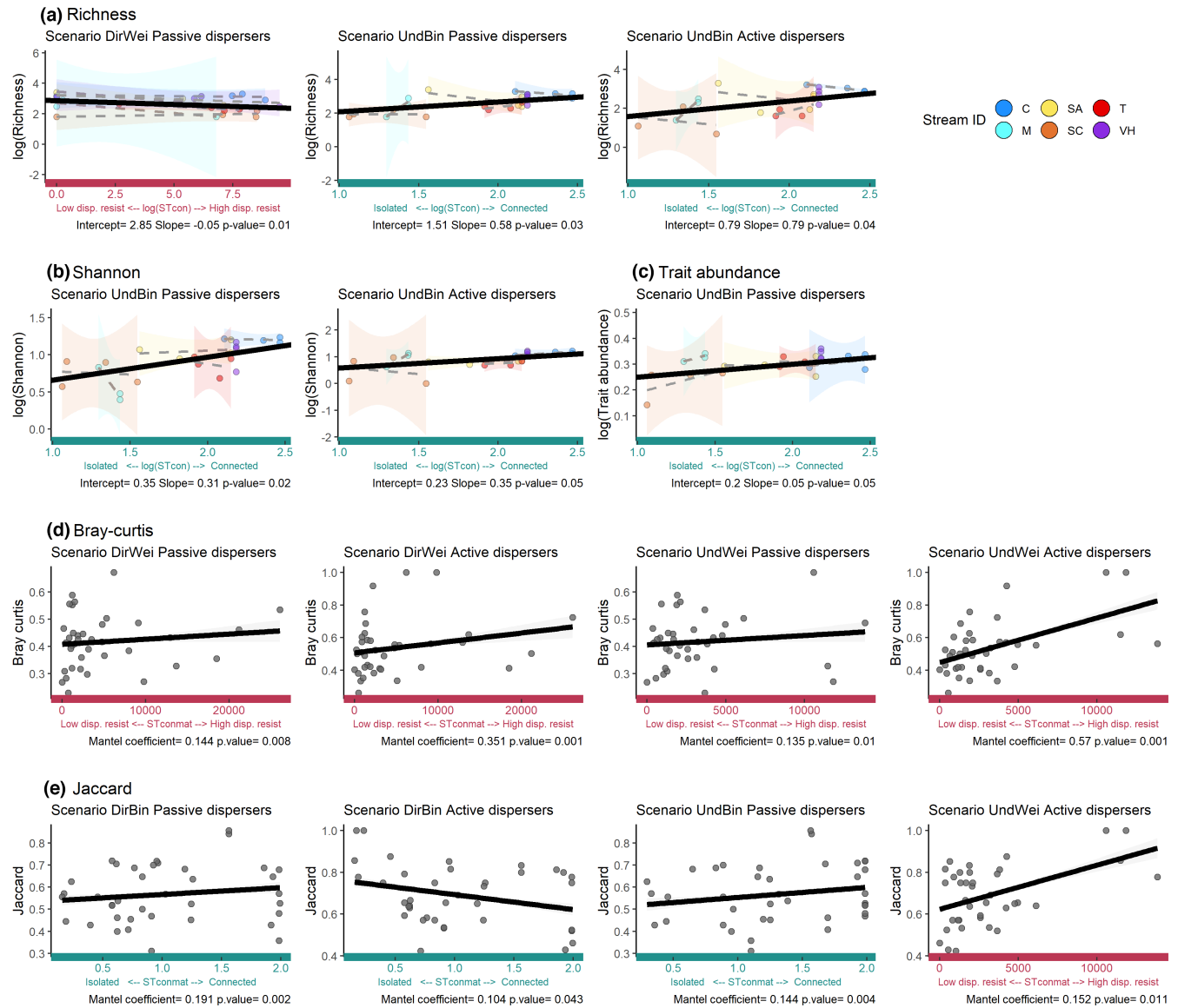
FIGURE 5 Significant linear mixed models between *STcon* (a–c) and *STconamt* (d, e) and biological metrics calculated for passive aquatic and active aerial dispersers. (a) Richness, (b) Shannon, (c) Trait abundance, (d) Pairwise metrics (i.e. Jaccard and Bray–Curtis indices). Note that *STcon* values for DirBin and UndBin scenarios (green *x* axes) quantify how much a site has been connected, whereas values for UndWei and DirWei scenarios (red *x* axes) quantify the dispersal resistance of each site. All the data are calculated based on the time window between the beginning and the sampling date (480 days). See all other results for all the metrics and scenarios in Figure S6.

Overall, although the study sites were close to each other (mean distance between sites within a stream was around 1 km and all the streams were located within an approximate range of 100 km²), the macroinvertebrate communities showed significant responses to spatiotemporal connectivity. This highlights the importance of quantifying spatiotemporal connectivity in highly dynamic systems such as temporary streams (Cid et al., 2020; Datry et al., 2016). Finally, *STconmat* proved useful to incorporate pairwise metrics (e.g. beta diversity calculated with Jaccard or Bray–Curtis indices) within spatiotemporal analysis of temporary systems (Khattar et al., 2021; Legendre & De Cáceres, 2013), which is key to better capture assembly processes or improve management of spatiotemporally variable

ecosystems (Bo et al., 2020; Boyé et al., 2019; Lamy et al., 2015; Ruhí et al., 2017; Sobek et al., 2009).

In dendritic networks such as fluvial systems, connectivity has been acknowledged for a long time as a key driver of diversity and functioning at population, community and/or ecosystem levels (Fullerton et al., 2010; Vannote et al., 1980). Indeed, several indices have been developed to assess the degree of fragmentation generated by dams (Baldan et al., 2022; Cote et al., 2009) or connectivity indices accounting for longitudinal and lateral connectivity (Rivers-Moore et al., 2016). However, the inclusion of both spatial and temporal connectivity facets has been poorly explored so far (Fullerton et al., 2010; Uroy et al., 2021). We believe that the proposed framework represents a first step towards a better inclusion

of spatiotemporal connectivity in general ecology, extending beyond our study case and being potentially applied to any ecosystem. For example, our measures could be useful to incorporate network connectivity into biodiversity conservation using systematic planning approaches (Hermoso et al., 2012). Also, *STcon* and *STconmat* can serve to assess the effectiveness of restoration measures as the community response to habitat restoration will depend on spatiotemporal connectivity to some extent (Cid et al., 2022). At the same time, it complements other methods like remote sensing (Bishop-Taylor et al., 2017) by specifically quantifying spatiotemporal dynamics and incorporating multiple time windows.

Overall, the proposed framework has a strong potential to be used at several temporal scales (e.g. days, months, years) and across different levels of biological organisation (e.g. populations, communities, ecosystems). Besides flow state, other metrics that vary spatiotemporally and define connectivity such as land use could be used (Firmiano et al., 2021). Furthermore, the current function could be extended to include other network structures by defining the number of neighbours at which dispersal is considered effective, either setting distance thresholds or dispersal decay with distance (Borthagaray et al., 2015; Muneepeerakul et al., 2008; Radinger & Wolter, 2014). In addition, another aspect that could be further developed within this framework is related to antecedent spatiotemporal connectivity (i.e. the temporal scale considered by *STcon* and *STconmat*). In the approach presented here, the ST matrix considers the spatial structure from the previous day, thereby considering two time steps (i.e. what happened on day 1 has an impact on day 2 but not on day 3; Uroy et al., 2021). Both the defined network structure and the time span are case-specific and could be adjusted to the characteristics of the studied system and the focal organism (e.g. organism life span, a pollution event). So far, the main limitation of this framework is still the lack of databases that include high spatial and temporal resolutions at relevant scales. Furthermore, the adaptation of the framework to different ecosystems and network structures should be made with caution. For example, the parameters used to calculate *STcon* and *STconmat* need to be defined for each system, because the results can be considerably different depending on the designed scenario. Nonetheless, the adaptability of our framework suggests that it can still be expanded to incorporate more facets of the interaction between spatial and temporal processes. In this regard, we provide the R code (see Supporting Information, Cunillera-Montcusí, 2023) to facilitate and promote future studies.

The quantification of spatiotemporal connectivity is key for any ecosystems subjected to high seasonal and/or interannual variability, or affected by natural (e.g. wildfires, hurricanes, floods, droughts) or human-driven disturbances (e.g. invasive species, point source pollution). Moreover, environmental conditions are becoming globally harsher and more variable, with an expected increase in the frequency, duration and variability of natural and human-driven disturbances (IPCC, 2022). Consequently, we need to further explore and develop frameworks that can capture such variability in space and time (Uroy et al., 2021). To guide future conservation and management actions (Chase et al., 2020; Cid et al., 2020; Schiesari

et al., 2019). We encourage the inclusion of spatiotemporal connectivity in future studies in the field of meta-system ecology, restoration ecology and biodiversity conservation to test and challenge our method so we can gain insights into spatiotemporal processes.

AUTHOR CONTRIBUTIONS

David Cunillera-Montcusí conceptualised the framework and leaded the paper in the analysis, writing, interpretation and edition. Miguel Cañedo-Argüelles and Núria Bonada conceptualised the study, collected the data, interpreted the results, wrote and edited the manuscript. Núria Cid collected the data, interpreted the results, wrote and edited the manuscript. José María Fernández-Calero, Sebastian Pölster, Roger Argelich and Pau Fortuño collected the data and edited the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare none.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14105.

DATA AVAILABILITY STATEMENT

All data used in this work as well as the corresponding code and the function to calculate STcon and STconmat values are available at Cunillera-Montcusí (2023) and a tutorial to illustrate the usage of the function *spat_temp_index* is available at https://cunillera-montcusi.github.io/Quantifyinig-SpaTem-connectivity/.

ORCID

David Cunillera-Montcusí https://orcid.org/0000-0001-8666-346X

José María Fernández-Calero https://orcid.org/0000-0003-0095-1765

Núria Cid https://orcid.org/0000-0002-9997-5523

Núria Bonada https://orcid.org/0000-0002-2983-3335

Miguel Cañedo-Argüelles https://orcid.org/0000-0003-3864-7451

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Maps of the main study area located in Sant Llorenç del Munt i l'Obac natural park and of each one of the monitored streams with the sampling locations and data loggers deployed to monitor flow states. Castelló (C), Mura (M), Rellinars (R), San Ana (SA), Santa Creu (SC), Talamanca (T) and Vall d'horta (VH). Note that the number of data loggers deployed in each stream varied due to differences in stream morphology and the number of reaches that were normally dry in that stream.

Figure S2: Network representation of all monitored streams C, M, R, SA, SC, T and VH respectively. Two network structure were considered: (a) directed, which was used for the DirBin and DirWei scenarios and (b) undirected, which was used for the UndBin and UndWei scenarios.

Figure S3: STcon and STconmat graphical representation for the seven monitored streams: C, M, R, SA, SC, T and VH respectively. The four calculated scenarios are represented in each part: DirBin; DirWei; UndBin; UndWei. The viridis colour gradient and arrow size illustrates the corresponding values of STcon and STconmat. For DirBin and UndBin scenarios a gradient from purple/blue to green/yellow indicates high to low spatiotemporal connectivity respectively. For DirWei and UndWei a gradient from grey/purple to red/yellow indicates greater or lower spatiotemporal resistance to dispersal. Binary and Weighted scenarios quantify differently connectivity as they focus on only number of connections or how big is the distance to be connected.

Figure S4: Spearman correlation matrix including STcon values calculated for the four scenarios DirBin, DirWei, UndBin, and UndWei. Spearman rho values for each pair are represented in the upper triangle section of the plot. Pairs with a significant correlation were indicated with a black asterisk next to Spearmen correlation rho.

Figure S5: STcon values for each stream and for each one of the four scenarios. (a) DirBin, (b) DirWei, (c) UndBin, (d) UndWei. Note that these plots represent the same values as Figure 4 but here they are shown for each individual stream.

Figure S6: All community metrics results for the six monitored streams from which enough biological data was obtained (the R stream was not considered here). Each box corresponds to an individual community metric: (a) Taxonomic Richness, (b) Shannon Wiener-diversity, (c) Trait abundance, (d) Jaccard dissimilarity, and (d) Bray Curtis dissimilarity. In each box, the first row of plots correspond to active dispersers (group of trait f4) and the second row of plots to passive dispersers (group of trait f1). Note the *X* axes of plots must be read carefully for each scenario: for DirBin and UndBin higher STcon values mean higher spatiotemporal connectivity whereas for DirWei and UndWei higher STcon values mean greater spatiotemporal resistance to dispersal.

Table S1: STcon and STconmat values for each one of the monitored sites (Codi_HOBO) with their corresponding coordinates, the ID of the stream, the position in following an Uo- to Downstream (DtoU) for each of thef four scenarios considered: DriBin, DirWei, UndBin and UndWei.

Table S2: Linear mixed models results for each one of the community metrics calculated: (a) Taxonmic richness; (b) Shannon-Wiener index; (c) Trait abundance; (d) Jaccard dissimilarity and (e) Bray–Curtis dissimilarity. For each metric, the results for each one of the four scenarios (DirBin, DirWei, UndBin, UndWei) is reported together with the dispersal group (Active and Passive dispersers). Note that significant results are highlighted in bold.