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RESEARCH ARTICLE

Simulating drying and human impacts on river networks to evaluate biological quality indices performance through the lens of metacommunity theory

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Abstract

1. Incorporating metacommunity perspectives into bioassessment represents a major challenge in managing drying river networks, where drying-induced fragmentation compromises the performance of biological indices to assess their ecological status. Current indices focus on local community responses to stressors and neglect the effect of regional processes, such as spatiotemporal connectivity and dispersal, on metacommunity assembly.
2. In this work, we explored the effect of drying on the performance of a widely used biological index IBMWP (Iberian Biological Monitoring Working Party) using metacommunity simulations on a synthetic drying river network. We assessed how different gradients of drying-driven fragmentation and human impact extent determine local richness and the biological index scores by combining simulations with biomonitoring information.
3. We used a coalescent metacommunity model to simulate the exchange of individuals between local communities along synthetic drying river networks subjected to different drying extent, intensity and human impact extent scenarios. Additionally, we considered two major characteristics for each simulated taxon: (i) tolerance to human impacts and (ii) dispersal strategy (flying, swimming or drifting).

Zeynep Ersoy and David Cunillera-Montcusí contributed equally to this work as first authors.

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4. For each simulation, we obtained local richness and the biological index value. Then, we calculated biological index performance, defined as the capacity to distinguish between impacted and non-impacted sites. Finally, we tested our approach in six non-impacted European drying river networks, with available drying information.
5. Our results showed that low spatiotemporal connectivity consistently led to decreased local richness and low index scores, reflecting poor biological quality. As drying extent and intensity increased, drying-induced fragmentation significantly reduced the biological index performance. With a 50% increase in drying extent, index performance fell around 60% and at high drying levels, it dropped more than 90%. This decay followed a convex pattern, with a marked drop as soon as drying appeared in the catchment and levelling off at higher drying extents.
6. *Synthesis and applications*. This work constitutes a first step towards developing simulation-based assessments that incorporate catchment drying patterns to support biomonitoring of drying river networks. Our approach can inform stakeholders when current methods are likely to fail and contribute to decision-making on whether adapting current methods is possible or developing new indices is necessary.

KEYWORDS
biomonitoring, connectivity, dispersal, drying river networks, macroinvertebrates, metacommunity, modelling, river management

1 | INTRODUCTION

River networks are increasingly subjected to drying due to global change pressures (Datry et al., 2023; Messager et al., 2021). Drying reshapes river networks at both spatial and temporal scales, affecting the number of reaches that contain water and how frequently they lose it. Together, these alterations reconfigure fluvial connectivity at the spatiotemporal level (Jacquet et al., 2022; Journiac et al., 2025). These changes concomitantly impact the exchange of individuals, species and the flux of matter across river segments (Arias-Real et al., 2023; Cid et al., 2022; Datry et al., 2023; Sarremejane et al., 2021), altering community assembly and ecosystem functioning (Holyoak et al., 2020; Journiac et al., 2025; Marco Palamara et al., 2023). Although the importance of these regional-scale drivers has been acknowledged, their influence on river management remains far from clear, challenging the conservation of drying river networks against current global threats (Cid et al., 2020; Datry et al., 2023; Sarremejane, England, et al., 2024; Soria et al., 2020).

River management practices, including biomonitoring, mostly focus on local-scale processes (i.e. environmental filtering), overlooking the key role that regional processes such as drying-driven fragmentation play in shaping diversity (Brodie et al., 2025; Chase et al., 2020; Cid et al., 2020; Heino et al., 2015). Consequently, traditional biomonitoring tools often fail to properly assess human impacts on drying river networks (Bonada et al., 2024; Ersoy et al., 2024; Soria et al., 2020). For instance, reaches that become isolated due to drying often have lower species richness despite favourable environmental conditions (Cañedo-Argüelles et al., 2015; Henriques-Silva et al., 2019). At the same time, highly connected sites may harbour greater richness even with suboptimal environmental conditions (Cañedo-Argüelles et al., 2015; Heino, 2013; Jabot et al., 2020). In this context, metacommunity perspectives (Leibold & Chase, 2017) can provide key insights for river conservation by incorporating not only local drivers but also habitat position within the network (Borthagaray et al., 2020; Heino, 2013; Heino et al., 2015; Thompson et al., 2017) and the different dispersal strategies of organisms (Milošević et al., 2022; Siqueira et al., 2014; Stojković Piperac et al., 2023). Several works have highlighted the importance of these drivers in determining species richness and biomonitoring indices in perennial rivers (Durães et al., 2016; Siqueira et al., 2014). Nevertheless, this interplay remains unexplored in drying river networks due to the complexity of quantifying the spatiotemporal scales at which drying shapes connectivity and, in turn, alters metacommunity dynamics (Courtwright & Hawkins, 2024).

The link between river biomonitoring and metacommunity theory has been primarily explored from a theoretical point of view in perennial networks (Heino, 2013; Patrick et al., 2021). The few existing conceptual frameworks focused on drying river networks expect a decline in the performance of biological indices with increasing drying, which is modulated by spatial connectivity and organisms' dispersal and resistance traits (Cid et al., 2020, 2022). Although considerable progress has been made in understanding how

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drying influences biodiversity from local to regional scales (Jacquet et al., 2022; Journiac et al., 2025), a mechanistic understanding of how drying may impact biological indices is still lacking. Within this context, the growing availability of hydrological data from drying river networks can be very useful, because it allows quantifying spatiotemporal connectivity (Cunillera-Montcusí et al., 2023; Mimeau et al., 2024; Pineda-Morante et al., 2022). Indeed, several works have already highlighted how variable spatiotemporal connectivity in drying river networks determines community diversity and ecosystem functioning (Chalmandrier et al., 2025; Fernández-Calero et al., 2024; Hárságyi et al., 2025). Thus, these advances open the window to assess the interplay between spatiotemporal connectivity and performance of biomonitoring indices (Bonada et al., 2024; Cid et al., 2020).

In this study, we assessed the effects of river network drying and human impacts on the performance of a widely used biological index, the Iberian Biological Monitoring Working Party (IBMWP; Figure 1). To do this, we coupled macroinvertebrate biomonitoring databases with metacommunity simulations incorporating organisms' dispersal across varying degrees of river drying (i.e. intensity and extent) and human impacts (i.e. extent). First, we investigated how local richness and the score of the biological index responded to the loss of spatiotemporal connectivity and widespread human impact extents. Second, we quantified the expected decay in biological index performance along gradients of drying (i.e. the relative difference between impacted and non-impacted reaches). Finally, to exemplify the connection between the current approach and real-case scenarios, we assessed the expected changes in biological index performance for six European drying river networks from which long-term drying patterns were available. Building on previous empirical works (Datry, 2012; Escobar-Camacho et al., 2025; Sarremejane, England, et al., 2020; Stubbington et al., 2024), our simulation approach represents the decrease in species richness and abundance linked to drying and relates these effects with human impacts on sensitive species. Thus, our simulation explores how the interaction between these two drivers will determine the score of the biological index. We expect that (i) the performance of the biological index will show a sharper decline when drying starts to fragment the river network (Courtwright & Hawkins, 2024). This drop will be driven by the drying-driven loss in spatiotemporal connectivity and its interplay with human impacts, which will increasingly favour tolerant taxa.

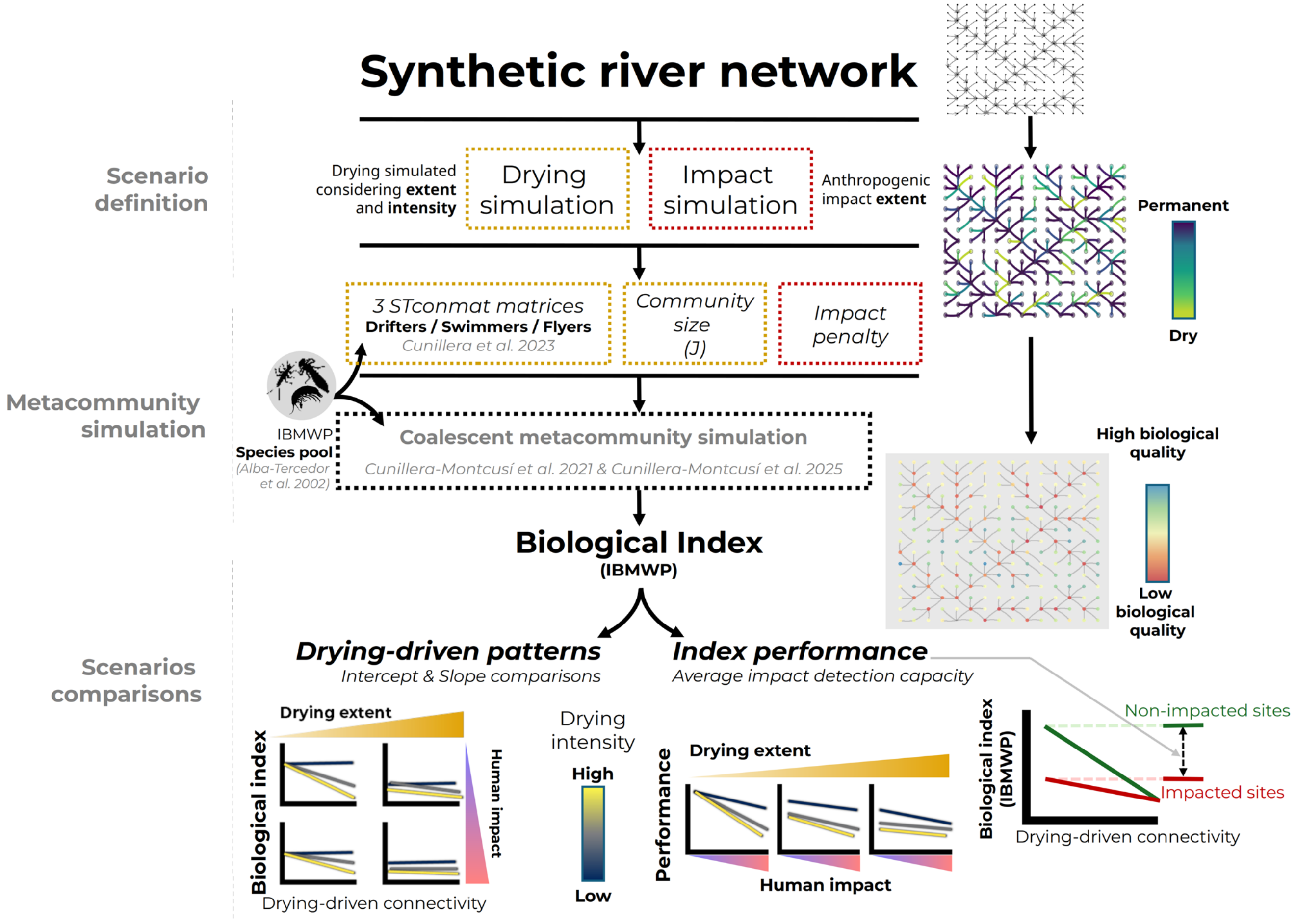

FIGURE 1 Overview showing the workflow to build the metacommunity simulations (Borthagaray et al., 2025; Cunillera-Montcusí et al., 2021, 2023, 2025) and analyse their outputs to compare different scenarios.

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Finally, we expect that (ii) the decline of the performance of the biological index will attenuate as drying and human impacts affect most of the river network as a consequence of environmental (i.e. human impacts) and drying-driven local (i.e. community size) and regional (i.e. fragmentation) metacommunity homogenization (Piano et al., 2020; Rolls et al., 2023). Through this work, we develop a novel approach to support intermittent stream management by identifying at which drying intensity and extension biological indices fail to adequately detect human impacts in drying river networks.

2 | MATERIALS AND METHODS

2.1 | Dendritic river networks

We generated a synthetic river network using the OCNet R package (Carraro et al., 2020), which represented our base template for simulating drying and human impact scenarios (Sections 2.2 and 2.3). We used the *create_OCN* function to generate an Optimal Channel Network (OCN) to simulate a realistic river network on a square lattice (15 × 15) with a cell size of 2 km. This resulted in a network of 225 nodes representing a catchment of 900 km^2 with a single outlet. This approach provides a standardized and replicable river network capturing the essential structure of a real mid-sized river and ensures computational capacity for posterior simulations. We used this generated river network in all posterior simulations to maintain a constant spatial configuration throughout all scenarios.

2.2 | Drying scenarios and connectivity metrics

To consider the impacts of drying on the connectivity of the river network (i.e. probability of dispersal between nodes), we simulated a range of scenarios by manipulating two parameters: drying spatial extent (i.e. number of drying nodes throughout the network) and drying intensity (i.e. length and frequency of drying). Drying spatial extent indicated the number of dry nodes, ranging between 3 (1%) and 203 (90%) nodes of a total of 225. We defined nine levels of drying extent covering a range of drying intensity from almost permanent to fully intermittent networks (1%, 10%, 25%, 35%, 45%, 50%, 65%, 75%, 90%). Drying intensity represented the variability in duration and frequency of drying for each node, ranging from homogeneous and less frequent drying (e.g. all dry nodes remain dry for 10% of the time) to heterogeneous and highly recurrent drying (e.g. dry nodes are divided into different categories, ranging between nodes drying 10% and 99% of the time). We defined eight levels of drying intensity that summarize this gradient from low to high drying intensity (0.1, 0.25, 0.5, 0.55, 0.65, 0.75, 0.9, 0.99). Following this framework, we built a flow state database spanning 48 time units (i.e. a matrix of 225 columns corresponding to each network node and 48 rows with the flow state wet (1)/dry (0) at each time). This matrix corresponds to a 2-year time period, which represents a biologically relevant temporal window for these systems (Chalmandrier et al., 2025) and does not compromise computational times (Cunillera-Montcusí et al., 2023). As the impact of drying on node connectivity depends on its location within the network (Jacquet et al., 2022; Sarremejane, England, et al., 2020), we always considered the same set of nodes as drying nodes to maintain comparability between drying scenarios of different spatial extents.

We calculated spatiotemporal connectivity matrices (STconmat) for each drying scenario, combining drying extent and intensity following Cunillera-Montcusí et al. (2023), averaging simulated spatial and temporal connections for each pair of nodes over the considered period. To calculate STconmat, we used a weighted network (as *DirWei* scenario in Cunillera-Montcusí et al., 2023), where node distances are considered as link weights and the presence of water facilitates dispersal (i.e. link weight decreases by 90%), while drying preserves the full Euclidean distance (i.e. link weight is equal to the distance between nodes). Overall, STconmat defines the connectivity matrix between all network nodes integrating nodes' topological position and drying effects on their connectivity (i.e. a dry node will decrease the connectivity of all paths crossing it). Thus, greater STconmat values imply higher dispersal resistance due to greater distance and dry-driven fragmentation (i.e. sites located far and/or isolated due to drying). Finally, we calculated STconmat for three different network structures corresponding to three major dispersal strategies extracted from Sarremejane, Cid, et al. (2020): aquatic passive (drifters), aquatic active (swimmers or crawlers), and aerial active dispersers (aquatic larvae with flying adults: flyers). For aquatic passive dispersers, we considered connectivity only from upstream to downstream. For aquatic active dispersers, we considered both upstream and downstream. For aerial active dispersers, we considered connectivity independently of the river network, only determined by Euclidean distance. Overall, STconmat values represented the potential for dispersal between any pair of sites by incorporating both distance-driven dispersal and network fragmentation caused by the defined drying scenarios.

2.3 | Human impact scenarios

We also incorporated human impacts on metacommunity dynamics, defined as local environmental filters. We simulated two levels of impact at the local level: (i) Impacted, where we applied a penalty to establishment probability using tolerance scores from a standardized biological index based on macroinvertebrates at the family level in the Iberian Peninsula (IBMWP index; Alba-Tercedor et al., 2002; Table S1) (ii) Non-impacted, where establishment probability was solely determined by connectivity. Human impact extent was defined as the number of impacted nodes throughout the network. Although this biological index was developed for the rivers in the Iberian Peninsula, it is calibrated to other European indices (Munné & Prat, 2009), which allows its use as a general

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example of a biological index for our simulation exercise. We explored several levels of human impact extent from 3 (1%) to 203 (90%) impacted nodes out of a total of 225 nodes and covering a gradient of different categories of impact extent (1, 10, 25, 35, 45, 50, 65, 75, 90%).

2.4 | Metacommunity simulations in response to drying and human impact scenarios

We assessed how the interaction between drying and human impact influenced local biodiversity patterns by running a coalescent metacommunity model on the synthetic river network (Borthagaray et al., 2025; Borthagaray, Cunillera-Montcusí, Bou, Biggs, & Arim, 2023; Borthagaray, Cunillera-Montcusí, Bou, Tornero, et al., 2023; Cunillera-Montcusí et al., 2021, 2025). This model simulated the exchange and establishment of individuals among nodes and along the river network, without accounting for biotic interactions (see Appendix S1). These simulations were determined by (i) the regional effects of drying on connectivity (i.e. STconmat), (ii) the local impacts of drying on community size (i.e. habitat decrease in carrying capacity) (Arias-Real et al., 2021; Datry, 2012; Greenwood & McIntosh, 2010; Sarremejane et al., 2021) and (iii) human impact penalty for the impacted sites. Using this model, we simulated metacommunity assembly considering the constraints imposed by each scenario (i.e. drying extent, intensity and human impact extent). For each metacommunity, we calculated total richness and biological index values for each node by adding family scores. We ran 10 replicates for each combination of scenarios and calculated their median to obtain an averaged value per scenario (see Appendix S1).

2.5 | Data analysis

We explored the linear relationships between STconmat and two metrics: local richness and biological index across all scenario combinations (i.e. drying extent, and drying intensity, human impact extent). We extracted the intercepts and slopes of these relationships to quantify the trends of these two metrics along the simulated gradients. We then assessed the performance of the biological index for each scenario (i.e. relative difference between impacted and non-impacted nodes), by using a single reference scenario corresponding to a non-impacted river (Human impact extent = 0.01) with low drying extent (Dry extent = 0.01) and low drying intensity (Dry intensity = 0.1) and representing the maximum potential index score values (i.e. the maximum difference between impacted and non-impacted sites). Then, we calculated the performance of the biological index as the ratio of change between impacted and non-impacted sites relative to this reference as follows:

$$\text{Performance} = \left(1 - \left(\frac{\text{Biological index}_{\text{Unimpacted}} - \text{Reference Biological index}}{\text{Biological index}_{\text{Impacted}} - \text{Reference Biological index}}\right)\right) \times 100.$$

Performance values near 100% will imply that there is a maximal difference between impacted and non-impacted sites relative to the reference score, indicating that the biological index can properly detect impacts. The lower the % value, the lower the capacity of the index to distinguish between impacted and non-impacted sites.

For each of the defined drying scenarios (i.e. combination of drying extent and drying intensity), we fitted a general linear model between performance and anthropogenic impact extent to analyse how performance was impacted by drying along the anthropogenic impact gradient. Finally, we used the drying patterns from six non-impacted drying river networks located throughout Europe (Spain, France, Croatia, Finland, Hungary and Czech Republic), from which daily drying information (site-level flow/dry state from January 2019 to 2021) was available at the catchment scale (Datry et al., 2021; Künne et al., 2022; Mimeau et al., 2024), to connect our simulations with real study cases. Details on each river network can be found at www.dryver.eu. Using this information, we quantified how the biological index performance would be impacted solely by drying in the river network, as these catchments are mostly non-impacted (anthropogenic impact set at 10%). We conducted all simulations and statistical analyses using R version 4.4.3 (R Core Team, 2025) and plotted graphs using the 'ggplot2' and 'viridis' packages (Garnier et al., 2023; Wickham, 2016).

3 | RESULTS

3.1 | Simulation and metacommunity outputs

In total, we generated 648 unique combinations of drying extent, drying intensity and human impact extent and simulated 10 different metacommunities for each combination ($n = 6480$ metacommunities). Overall, as drying extent and intensity increased, the spatial diversity of flow regimes (i.e. hydrological heterogeneity) increased (Figure 2). This was driven by the concomitant decrease in perennial sites (Figure S1A) and the emergence of more nodes presenting different drying frequencies (Figure S1B). These lead to a decrease in local community size (Figure S1C) and greater regional heterogeneity in spatiotemporal connectivity across scenarios (Figure S1D).

3.2 | Response along drying-induced fragmentation

Both local richness and the score of the biological index decreased as spatiotemporal connectivity decreased (Figure 3; Figures S2 and S3). Thus, as a site became more isolated and smaller due to drying, its local richness and biological index scores decreased (Figure S4A). This pattern was clear under a low human impact

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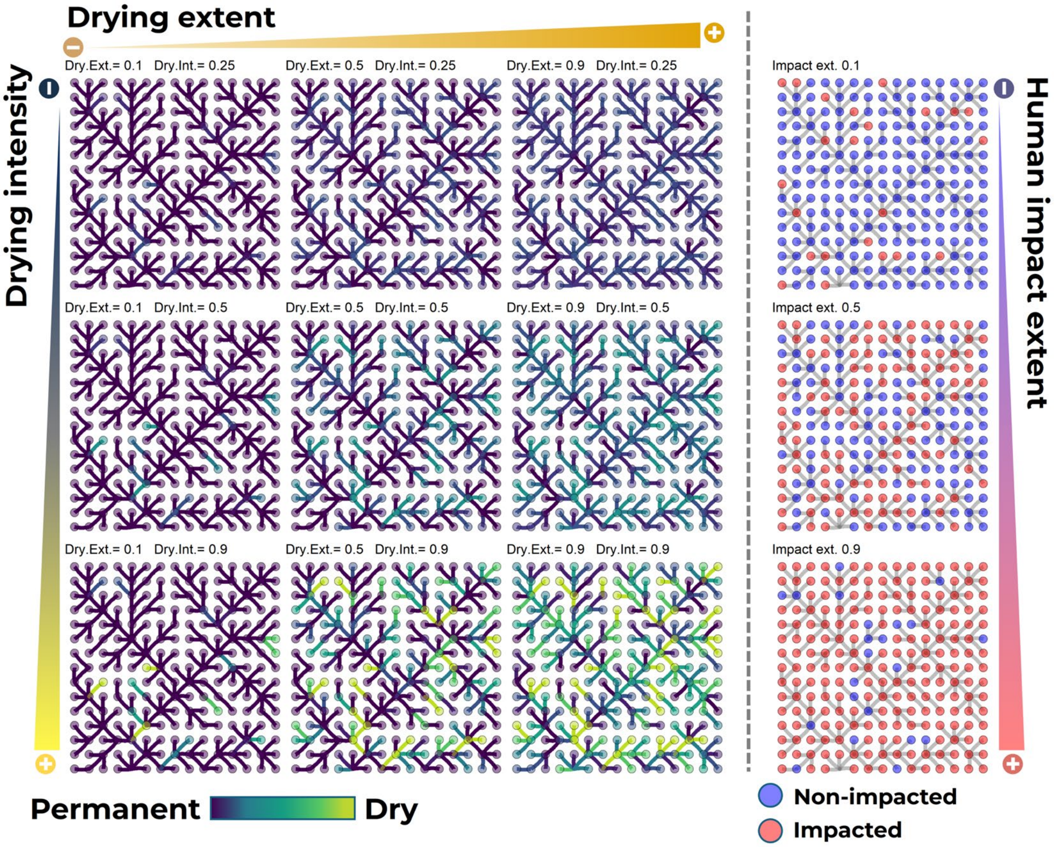

FIGURE 2 Examples of varying drying extent (Dry.Ext) and intensity (Dry.Int) and human impact extent scenarios (Impact.ext). The blue-green-yellow gradient illustrates the spatial configuration of water permanence across sites within the river network. The red and blue colours (right column) indicate impacted and non-impacted sites, respectively.

extent (Figure 3, top row). As drying intensity increased, the slope of the relationship between the biological index and spatiotemporal connectivity increased in magnitude, implying a stronger decrease in the scores of the biological index (i.e. the more frequently the river dried, the stronger its negative effect on index values; Figure 3 top row panels, Figure S4B). However, as drying and/or human impact extent increased, these negative relationships disappeared and the effect of spatiotemporal connectivity faded (i.e. intercept decreased and slopes flattened; Figure 3 from top to bottom panels, Figure S4B). This occurred because widespread drying and human impact extent resulted in low scores of the biological index across all sites, masking the negative effect of spatiotemporal connectivity (e.g. when most sites are greatly isolated, small and impacted, they present similarly low index values). Therefore, as drying and human impact extents increased, all sites became equally taxa-poor, regardless of their connectivity (Figure 3, bottom panels). As a consequence, the difference between impacted and non-impacted sites became negligible, leading to a failure to distinguish them and the concomitant decrease in performance.

3.3 | Biological index performance across scenarios

Drying-induced fragmentation and the greater extent of human impact resulted in a decrease in the performance of the biological index, as indicated by smaller intercept values (Figure 4; Figure S5). The negative slope between performance and human impact extent was modulated by drying extent and intensity (Figure 4; Figure S6). As drying extent increased, the decrease in intercepts suggested a reduced performance of the biological index (Figure 4). For example, under non-impacted conditions (i.e. 1% human impact extent), an increase in drying extent from 10% to 25% reduced average performance by 13% (from 75% to 62%, respectively, after averaging all drying intensities), while the same increase from 75% to 90% reduced performance by 4% (from 31% to 27%, respectively, after averaging all drying intensities). We observed a more extreme change with the increasing drying intensity. In scenarios with low drying extent, performance was only reduced by human impact extent (i.e. all lines decrease together, Figure 4, left panel). However, as both the drying extent and intensity increased, they overrode the effect of human impact by lowering the scores of the biological index

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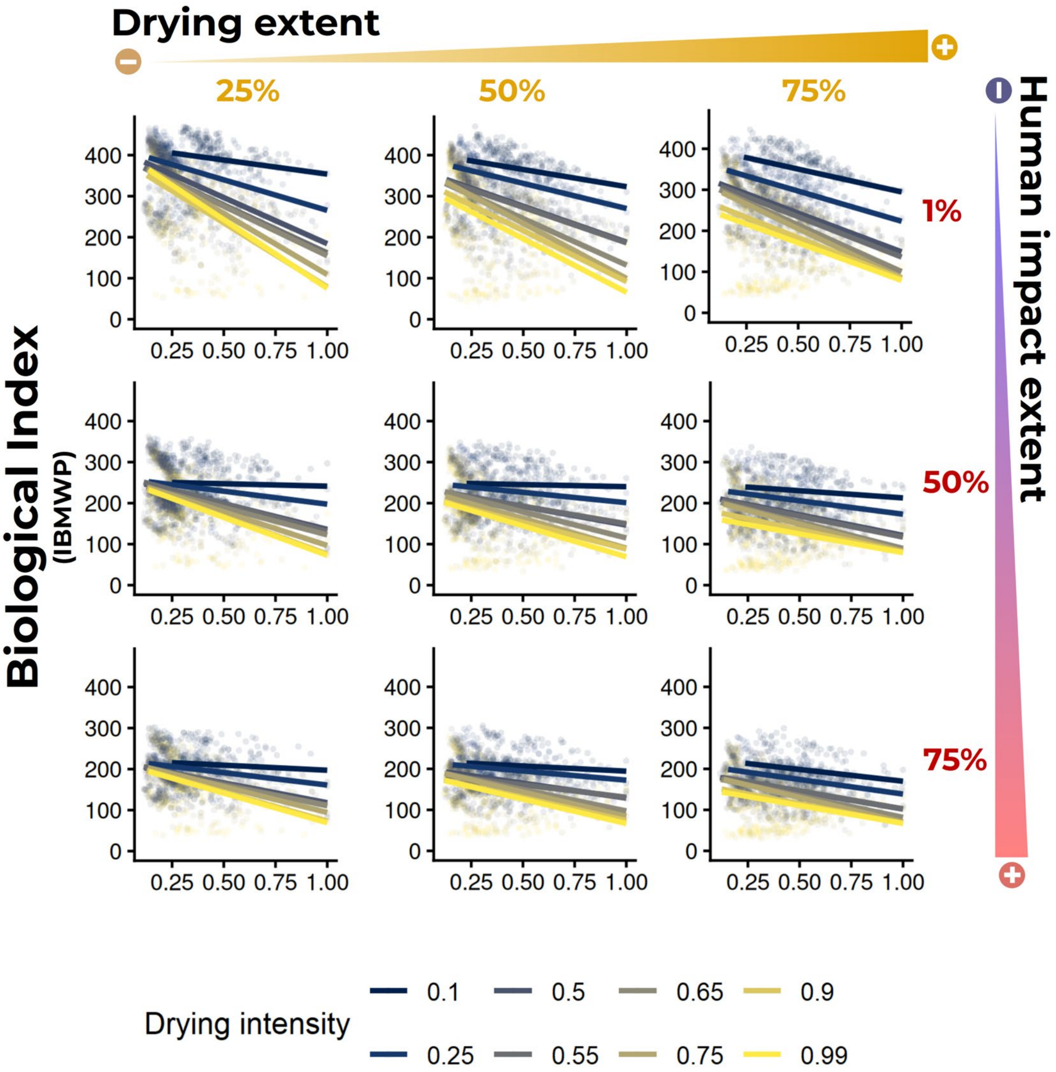

FIGURE 3 Linear relationships between the biological index (IBMWP) and the dispersal resistance. Sites with high dispersal resistance are strongly isolated due to distance and drying (STconmat). Each panel corresponds to a combination of scenarios of drying extent (25%, 40%, 75%), and human impact extent (1%, 50%, 75%). For each combination, the considered drying intensities are represented as a linear trend (blue to yellow gradient).

across the network. As such, under non-impacted conditions (i.e. 1% of human impact extent) and 25% of drying extent, the difference between low and high drying intensity was around 47%, indicating the strong differentiation that drying intensity can also produce in intermediate scenarios. Under more extreme scenarios with high drying extent and intensity, the difference between impacted and non-impacted sites was consistently low, regardless of the degree of human impact extent (i.e. nearly flat slopes for most drying intensities in Figure 4).

3.4 | Coupling real drying patterns with simulated scenarios

Drying extent and intensity from six non-impacted drying river networks aligned well with the drying scenarios that we designed for the synthetic river network (Figure 5). In these river networks, drying extent (i.e. number of sites that dry) ranged from low to almost fully drying networks (Lepsämänjoki, 'A' = 30.30%, Bükkösdi, 'B' = 42.30%, Albarine 'C' = 55.53%, Butižnica, 'D' = 55.63%, Velička, 'E' = 64.23%, and Genal, 'F' = 84.41%). Similarly, drying intensity (i.e. the variability in drying length for all network sites) ranged from low to very high (A = 0.25, B = 0.65, C = 0.50, D = 0.99, E = 0.50 and F = 0.9). Under conditions of 10% human impact extent (Figure 5, see Figure S8 for the other human impact extents), the performance of the biological index rapidly decreased as a function of drying extent and intensity. Each river network showed different performance profiles, with the Genal river network (F) being the most extreme case, where performance dropped to 25% (Figure 5). Thus, for this river network, the capacity of the biological index to distinguish between impacted and non-impacted sites would be reduced by 75% solely due to its natural drying conditions. This decay in biological index performance was driven by both local (i.e. community size) and regional (i.e. STconmat) drying effects, particularly at high drying

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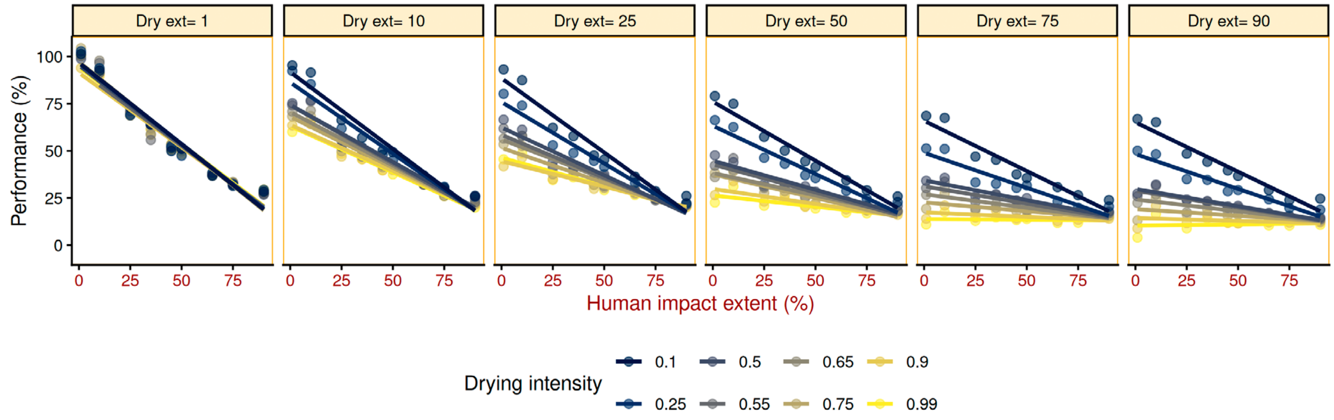

FIGURE 4 Linear relationship between biological index performance (%) and human impact extent (% of impacted sites) along selected drying extent scenarios and for different drying intensities (blue to yellow lines).

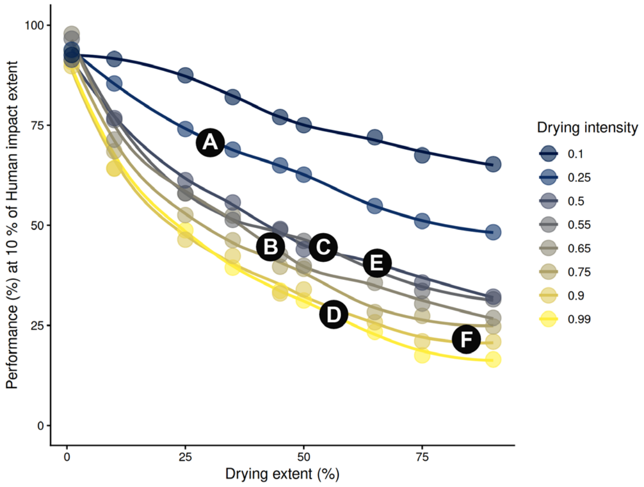

FIGURE 5 Biological index performance along the drying extent gradient (%) and for different drying intensities (coloured lines and dots) under a 10% human impact extent. Lines represent smoothed trends fitted using the LOESS method to visualize the decay pattern. Dark circles indicate the position that would correspond to the six non-impacted European drying river networks according to their drying extent and intensity (A–F). From left to right, Lepsämänjoki catchment, Finland ('A'), Bükkösdi catchment, Hungary ('B'), Albarine catchment, France ('C'), Butižnica catchment, Croatia ('D'), Velička catchment, Czech Republic ('E') and Genal catchment, Spain ('F').

intensities and extents, where community size markedly decreased for most nodes in the network (see Appendix S2).

4 | DISCUSSION

Our simulations revealed the multifaceted interaction of drying and human impacts on biological index performance across spatial and temporal scales (i.e. extent and intensity). Incorporating both local (i.e. smaller community size) and regional (i.e. network fragmentation) drying effects allowed us to reproduce drying-driven effects on fluvial metacommunities (Chalmandrier et al., 2025; Crabot et al., 2020; Escobar-Camacho et al., 2025; Journiac et al., 2025). In parallel, we related these effects to human impacts, simulating how their interaction shapes biological index scores (Cid et al., 2020). While drying extent acted as a regional modulator defining the maximum local richness (Cunillera-Montcusí et al., 2025; Riva & Fahrig, 2023; Zhang et al., 2024), drying intensity defined the rate at which local richness was lost in response to drying-driven fragmentation, which increased as the intensity increased. This trend aligns with previous regional and large-scale studies that showed how drying duration and frequency diminish local diversity and abundance (Arias-Real et al., 2021; Datry, 2012; Escobar-Camacho et al., 2025; Pineda-Morante et al., 2022; Sarremejane, England, et al., 2020). In line with our hypotheses, index performance drastically dropped as soon as drying started, with a 40% decrease under a 25% drying extent. Then this trend levelled off as drying extent continued to increase, with a decrease of around 60% in performance above 50% of the drying extent. Above this extent, impacted and non-impacted sites would be similarly classified by the biological index, leading to the failure of any monitoring assessment. This aligns with the expectation that the drying effects on community composition would be indistinguishable from human impacts, as taxa tolerant to drying are often also tolerant to human impacts (Cid et al., 2020). The value of our approach is that it serves to identify the levels of drying at which biological indices fail to capture changes in the biological quality associated with human impacts for a given catchment. This opens the question of what to do in such cases, with the design of new indices (e.g. terrestrial arthropods as in Sánchez-Montoya et al., 2020) that are able to disentangle the effects of drying from the effects of human impacts being the next logical step (Cid et al., 2020; Datry et al., 2023; Ersoy et al., 2024; Soria et al., 2020). Focusing only on local niche-based approaches constitutes a weakness for traditional biological indices when regional-scale processes such as species dispersal can be affected by changes in river network connectivity resulting from drying (Courtwright & Hawkins, 2024; Haase et al., 2023). Therefore, a metacommunity perspective has been proposed to integrate local

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and regional scales (Chase et al., 2020; Cid et al., 2020). This approach aligns with empirical research showing that community assembly is driven by local and regional factors acting simultaneously (Astorga et al., 2011; Göthe et al., 2017; Heino, Soininen, et al., 2017; Murray-Stoker & Murray-Stoker, 2020). Yet, spatiotemporal connectivity of drying river networks can be diverse and generate a wide variety of configurations (Datry et al., 2023; Journiac et al., 2025; Sarremejane, Silverthorn, et al., 2024). This inherent complexity concomitantly impacts biological index performance, which changes greatly depending on drying extent or intensity. For example, while 50% drying extent implied around a 25% drop in performance in low drying intensity scenarios, the same drying extent in high drying intensity scenarios resulted in almost a 75% drop in performance. Our approach can cover a wide range of drying scenarios and adapt to real drying river networks when surface water permanence information is available (Messager et al., 2021; Mimeau et al., 2025). Therefore, rather than providing a unique answer to the question of 'when will biological indices fail?', our approach can measure the expected degree of failure of a specific biological index along different gradients of stress for a given catchment. This logic builds on the method proposed by Cid et al. (2020), which used biological traits, regional connectivity and flow regime in a model to predict index performance. Here, we advanced these ideas by using simulations to represent local and regional drying effects on these highly dynamic ecosystems (Cunillera-Montcusí et al., 2023; Datry et al., 2016; Journiac et al., 2025).

Our model confirms the predictions suggested by Cid et al. (2020), showing that the index performance follows a convex decay, which became more negative as drying intensity increased. This decay pattern in index performance is caused by the fragmentation of the network, which reduces dispersal between habitats (Fournier et al., 2023; Sarremejane, Silverthorn, et al., 2024), but also by the increased homogenization of communities generated by the dominance of species able to survive in these scenarios (Cid et al., 2020; He et al., 2020; Heino, Alahuhta, et al., 2017). These two drivers were captured by our simulations through (1) the concomitant decrease in community size and spatiotemporal connectivity, resulting in smaller carrying capacities and increased dispersal resistance, and (2) the homogenization linked to human impact extent that favoured the dominance of tolerant taxa (Alba-Tercedor et al., 2002). This was reflected in the progressive drop in performance as human impact extent increased, concomitantly increasing the similarity between impacted and non-impacted communities due to mass effects (i.e. increased presence of tolerant taxa across the network led to their dominance also in non-impacted habitats through dispersal). Although the decrease in the performance of the biological index when human impacts were widespread may seem counterintuitive, from a metacommunity standpoint, widespread human impacts may favour homogenization even in non-impacted sites. This is because of greater dispersal pressure from impacted sites, which resulted from source-sink dynamics (Horváth et al., 2025; Leibold & Chase, 2017; Savary et al., 2024). Indeed, these results were related to the species pool of our model, which was mostly composed of weaker dispersers that use the stream network as their main dispersal route (62% of the species pool), resulting in a convex decay pattern (Cid et al., 2020). Therefore, here we showed that the use of biological indices not adapted to drying underestimates true biological quality as soon as a small percentage of the catchment dries (i.e. a drop of 25% in performance with only 10% of the reaches drying). Such insights can benefit decision-making by determining the validity of biological indices and selecting what alternative approach could prove more effective (Courtwright & Hawkins, 2024; Steward et al., 2022; Wilding et al., 2018).

Drying river networks are still poorly managed in most cases, so novel biomonitoring approaches that capture spatiotemporal dynamics are urgently needed (Datry et al., 2016, 2023; Stubbington et al., 2024). This could be done by using non-impacted drying river networks as reference conditions and correcting for the drying effect on ecological quality assessment. However, categorizing drying river networks into defined compartments is risky, as it may only partially capture the complexity of these ecosystems (Chadd et al., 2017; Wilding et al., 2018). Such an oversimplification could, in turn, lead to a similar decrease in performance when conditions diverge from the defined reference (as in Figure S7). Other options include the use of new indices that incorporate terrestrial fauna inhabiting the dry riverbed (Bruno et al., 2022; Sánchez-Montoya et al., 2020; Sánchez-Nogueras et al., 2025; Stubbington et al., 2019) or fauna inhabiting river pools during the dry season (Ersoy et al., 2024). When catchment-level drying patterns are available (e.g. Mimeau et al., 2024), our approach could be used to simulate case-specific expected drops in performance (Blair, 2021; De Koning et al., 2023). This would provide a more individualized river network assessment of index performance that could help identify sites or scenarios with lower performance (Blair, 2021; Juarez et al., 2021). Therefore, the current approach advances the integration of drying river networks' natural complexity and facilitates a more realistic assessment that can result in improved monitoring, restoration and conservation of these ecosystems (Datry et al., 2023; Stubbington et al., 2022).

In this study, we used a metacommunity model that simulates the exchange of individuals between habitats following a determined network structure (Borthagaray, Cunillera-Montcusí, Bou, Tornero, et al., 2023; Cunillera-Montcusí et al., 2021). While such an approach has proven useful for capturing spatially driven assembly patterns (Borthagaray, Cunillera-Montcusí, Bou, Biggs, & Arim, 2023; Cunillera-Montcusí et al., 2025), it simplifies reality by neglecting biotic interactions (Alahuhta et al., 2025; McIntosh et al., 2017), topographic and land use-related landscape barriers (Cañedo-Argüelles et al., 2015; Firmiano et al., 2021) or drying resistance traits (Cid et al., 2020; Sarremejane et al., 2021; Tolonen et al., 2019). In this regard, Cid et al. (2020) hypothesized that resistance to drying would lead to different decay trends in performance. Similarly, disconnected pools can influence the survival of determined species, yet their effects are dependent on pool characteristics and the species' tolerance to more lentic conditions (Bonada et al., 2020; Ersoy et al., 2024; Soria et al., 2020). Our simulation did not include such cases, which could be included assuming that

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some species remain unaffected when a site dries. However, the lack of robust data on resistance traits and the interaction of these traits with human impacts (i.e. biological index scores) was beyond the scope of this work and deserves further study. For example, the role of resistance strategies (Doretto et al., 2020; Hershkovitz & Gasith, 2013; Strachan et al., 2014) and the influence of community structure in drying pools or prior to drying, also known as community disassembly (O'Neill, 2016), are interesting topics for future studies. In contrast, the availability of biological indices that quantify the degree of tolerance to human impacts allowed us to explore the interaction between drying and human impacts. This information enhanced the realism of the simulations by incorporating key functional aspects in response to local-scale stressors, which in turn interacted with different dispersal strategies reflecting organisms' regional-scale responses (Cunillera-Montcusí et al., 2021; Jacquet et al., 2022).

Despite the limitations mentioned, the current approach improved our understanding of the interactive effects of natural drying and human impacts on the performance of the biological index for both simulated and real drying river networks. While previous simulations explored the interplay between drying and diversity in drying river networks (Jacquet et al., 2022; Journiac et al., 2025), our work adds a novel layer of information by incorporating human impacts (Alba-Tercedor et al., 2002). In this line, our approach could easily be adapted to other aquatic organisms such as diatoms, fish or terrestrial invertebrates from dry riverbeds (Sánchez-Montoya et al., 2016, 2020) by considering their dispersal capacities, ecological niche and any other ecological characteristic that determines their responses to human impacts. The combination of these simulations would advance towards more complex digital tools, able to realistically simulate ecosystem dynamics (De Koning et al., 2023).

Overall, we assessed the role that drying plays in altering biological index performance by modelling metacommunity dynamics—that is, dispersal limitation and community size—as well as family-based functional traits—that is, dispersal strategies and tolerance. In this sense, our approach represents a foundational step towards developing models acknowledging the dynamics of drying river networks by challenging niche-based approaches and developing tools to support monitoring and conservation (Chase et al., 2020; Cid et al., 2020; Datry et al., 2023). The increasing availability of high-resolution data from new technologies and citizen science can provide a more accurate vision of spatiotemporal connectivity in these dynamic systems, allowing catchment-specific assessments (Fernández-Calero et al., 2024; Pineda-Morante et al., 2022; Truchy et al., 2023). Such high spatiotemporal resolution enables the development of more realistic simulations for drying river networks, as demonstrated in this study. These models can support decision-making and future scenario simulations while accounting for fluvial metacommunity dynamics (Chase et al., 2020; Cid et al., 2020). The full potential of these tools remains to be unlocked, but they may prove essential for addressing future ecological and conservation challenges (De Koning et al., 2023; Maasri et al., 2022), helping ecologists and managers break current conservation halts (Haase et al., 2023).

AUTHOR CONTRIBUTIONS

Zeynep Ersoy, David Cunillera-Montcusí, Núria Bonada and Núria Cid conceived the ideas and designed the conceptual framework; Zeynep Ersoy and David Cunillera-Montcusí collected the data for simulations from the literature (equal contribution), analysed the data (equal contribution) and led the writing of the manuscript (equal contribution). Núria Bonada and Núria Cid provided supervision and critical review. Núria Bonada, Núria Cid and María Mar Sánchez-Montoya led the project funding this work. Zeynep Ersoy, David Cunillera-Montcusí, Martí Piñero-Fernández, Miguel Cañedo-Argüelles, María Mar Sánchez-Montoya, Núria Bonada and Núria Cid contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code are provided in the following public GitHub Repository: https://github.com/Cunillera-Montcusi/Model-Dry-Guadalmed and

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are archived in Zenodo Digital Repository: https://doi.org/10.5281/zenodo.19350608 (Cunillera-Montcusí et al., 2026).

STATEMENT ON INCLUSION

Our study brings together authors from a number of different countries, including scientists based in the country where the study was carried out. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent were considered from the beginning. Whenever relevant, literature published by scientists from the region was cited; efforts were made to consider relevant work published in the local language.

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SUPPORTING INFORMATION

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

Appendix S1: In the following lines, we define in detail the metacommunity model that we used for each simulation and its parameterization. This model has already been used in different publications, from which other detailed information can be obtained (Borthagaray et al., 2025; Cunillera-Montcusí et al., 2021, 2025).

Appendix S2: Sensitivity analyses comparing scenarios considering drying-driven and fixed community size.

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Table S1: Dispersal strategy based on DISPERSE database (Sarremejane et al., 2020) and IBMWP scores (Alba-Tercedor et al., 2004) for each taxon used in the IBMWP biotic index. Dispersal strategy trait values were averaged from all genera from the DISPERSE database. If the value for each dispersal category was higher than the mean, we used that dispersal category; otherwise, the same taxon was repeated with different dispersal strategies. dis1: aquatic passive, dis2: aquatic active, dis4: aerial active.

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