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The European freshwater landscape and hotspot areas of mass effects and regional connectivity

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Abstract

Aim: The maintenance of broad-scale connectivity patterns is suggested as a sustainable strategy for biodiversity preservation. However, explicit approaches for quantifying the functional role of different areas in biogeographic connectivity have been elusive. Freshwaters are spatially structured ecosystems critically endangered because of human activities and global change, demanding connectivity-based approaches for their conservation. Mass effects—the increase in local diversity by immigration—and corridor effects—the connections with distant communities—are basic and relevant mechanisms connecting diversity with landscape configuration. Here, we identified freshwater hotspots areas for mass and corridor effects across Europe.

Location: Europe.

Methods: Using satellite images, we quantified the areas of ephemeral, temporal and permanent freshwaters. The landscape structure of the freshwater ecoregions was represented as a directed-graph, and the link weights were determined by the distance between cells and the water cover. Three centrality metrics were used to rank freshwater areas with respect to their potential role in dispersal-mediated mechanisms. Out-degree represents the potential of an area to operate as a diversity source to other regions. In-degree reflects the importance that incoming dispersal may have in local diversity. Betweenness refers to the importance of local areas for connecting other distant areas.

Results: We detected great concentrations of source hotspots on the northern regions associated to lentic ecosystems, main European rivers acting as ecological corridors for all freshwaters, and a mixed distribution of connectivity hotspots in southern and Mediterranean ecoregions, associated with lentic and/or lotic systems.

Main Conclusions: We showed an explicit connection between landscape structure and dispersal process at large geographic scales, highlighting hotspots of connectivity for the European waterscape. The spatial distribution of hotspots points to differences in landscape configurations potentially accounting for biogeographic diversity patterns and for mechanisms that have to be considered in conservation planning.

David Cunillera-Montcusí and Ana I. Borthagaray contributed equally to this study.

KEYWORDS
biodiversity, dispersal, ecological corridors, ecoregions, Europe, source and sink areas, stepping-stone areas, waterscape

1 | INTRODUCTION

The current global biodiversity crisis is strongly influenced by human impacts on natural ecosystems (Cazelles et al., 2019; Didham et al., 2020; Ripple et al., 2019). Climate change, landscape fragmentation and habitat loss have been highlighted as being directly responsible for global biodiversity declines (Barnett & Belote, 2021; Haddad et al., 2017; Leibold & Chase, 2018; Urban & Keitt, 2001). Notably, all these drivers imply the loss of broad-scale connectivity patterns (Carroll et al., 2018; Dinerstein et al., 2019; Marrec et al., 2020). The maintenance of the landscape connectivity has been suggested as a climate change adaptation strategy for biodiversity preservation and management (Game et al., 2011; Krosby et al., 2015), which allows species to track changing habitat conditions (Carroll et al., 2018; Game et al., 2011). Moreover, the Convention on Biological Diversity (CBD) has recommended the creation of well-connected networks to mitigate threats to biodiversity as a global conservation priority (Álvarez-Romero et al., 2018; Dinerstein et al., 2019; Saura et al., 2018). Thus, identifying regions that play a key role in maintaining landscape connectivity remains of the outmost importance to prevent ecosystems and populations from becoming isolated, preserving global biodiversity (Barnett & Belote, 2021; Carroll et al., 2018; Dinerstein et al., 2019; Ward et al., 2020; Wood et al., 2022). In this context, quantifying the functional role of different areas for alternative dispersal processes is an urgent challenge.

The landscape connectivity pattern delineates the potential routes for multiple species to disperse at broad scales (Barnett & Belote, 2021). In addition, basic ecological mechanisms could be linked to these connectivity patterns at large geographic extents. The flow of individuals through the landscape may impact biodiversity by mass effects, in which source communities enhance the diversity of sink communities (Brown & Kodric-Brown, 1977; Leibold & Chase, 2018; Shmida & Wilson, 1985). Large patch sizes and/or central locations in the landscape foster communities to act as a source of individuals to other communities, such that these communities have a disproportionately large role in determining diversity patterns at the landscape level (Carroll et al., 2018). Complementary to mass effects, some locations may have a large role in maintaining spatial diversity because they are required to connect distant regions of the landscape—i.e., the corridor effect (Haddad et al., 2011, 2014; Keitt et al., 1997). Theoretical and empirical evidence consistently supports these mass effects and corridor effects as basic and relevant mechanisms connecting diversity with landscape configuration (Hanski, 1999; Li et al., 2021; Saura et al., 2014). These mechanisms may be particularly relevant at large geographical scales where the connections among distant communities involve the interchange of individuals with larger taxonomic and functional differences (Carroll et al., 2018; Soininen, 2016). Consequently, assessing the roles of local regions at a continental scale beyond geopolitical boundaries is emerging as a main challenge in advancing the understanding of global biodiversity patterns and their management (Barnett & Belote, 2021; Dallimer & Strange, 2015).

A network-based approach has been used to quantify the landscape features directly connected to regional processes that may impact biodiversity patterns (Barnett & Belote, 2021; Carroll et al., 2018; Keitt et al., 1997; Urban & Keitt, 2001). This involves resuming the size and spatial distribution of the habitats and their connections as weighted graphs, in which nodes represent local areas and connections represent the potential flow of individuals among them (Borthagaray et al., 2014, 2020; Cunillera-Montcusí et al., 2021; Economo & Keitt, 2010). Representing the landscape structure as a spatial graph allows the estimation of graph-centrality metrics directly connected with the mass effects and corridor effects of local communities (Saura et al., 2014; Urban & Keitt, 2001). These metrics enhance our ability to identify core areas and priority ecological corridors for preserving some dispersal-mediated mechanisms that determine global biodiversity (Carroll et al., 2018).

Specifically, the landscape structure could be represented by a weighted and directed graph, with link weights estimated as a function of the distance between cells and the water cover of the source cell, for example the incidence function of Hanski (1999). In this graph, the basic mechanisms connecting landscape dispersal with the global biodiversity pattern could be thought of in terms of three centrality metrics (Figure 1). In this sense, we could quantify the relevance of each community either as a 'source' for their neighbours—out-degree centrality—a 'sink' receiving immigration from its neighbours—in-degree centrality—or a 'stepping-stone' being key for the regional movement between communities—betweenness centrality—(Newman, 2018). Despite being an abstract description of a system, graph-based analysis may reveal emergent properties of landscape structure that would not be evident otherwise (Carroll et al., 2018).

Freshwater ecosystems are the most endangered natural systems in the world (Abell et al., 2008; Dudgeon et al., 2006; IPBES, 2019). Species loss, habitat degradation and the lack of water are among the most evident consequences of the degradation of these ecosystems. Because of geo-political reasons, freshwater ecosystem management has been mainly focussed on local or country scales that do not match the scale of climate change projections (Dallimer & Strange, 2015; Szabolcs et al., 2022). However, maintaining landscape connectivity is the most frequently mentioned climate change adaptation strategy for biodiversity conservation (Game et al., 2011; Ward et al., 2020), and freshwater ecosystems are not an exception (see Hermoso et al., 2011). Additionally, ecological connectivity is a high priority for conservation planning and freshwater

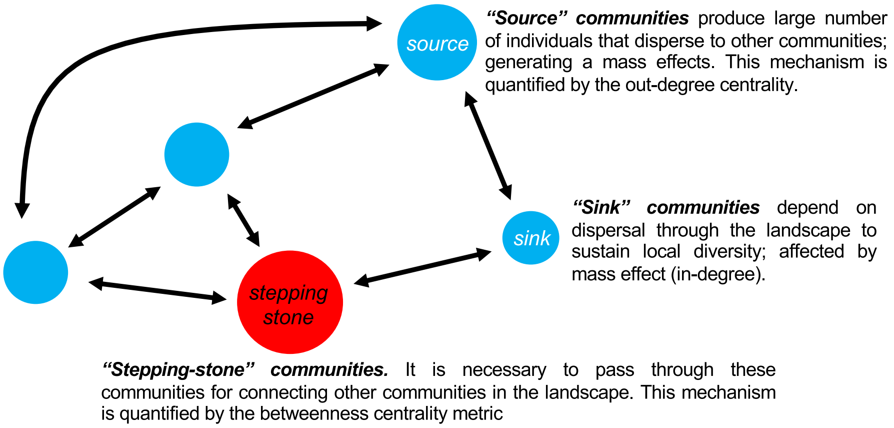

FIGURE 1 Mass effects and corridor effects—steppingstone—and their relationships with the centrality metrics out-degree, in-degree and betweenness. Landscape structure is represented by a directed and weighted graph. Each node in the graph is a local community (i.e. water body), and each link represents the flow of individuals between communities, which is proportional to the area occupied and the distance between communities (black arrows).

management in the post-2020 global biodiversity framework (van Rees et al., 2021). Freshwater environments comprise a wide range of ecosystems—ponds, streams, lakes, wetlands and rivers—with many species that are shared among them (Biggs et al., 2017; Hill et al., 2021). Furthermore, the coupling by individual dispersal of these different types of environments was identified as a potential determinant of freshwater biogeography (Borthagaray et al., 2023), and consequently, should be recognized when freshwater connectivity is considered.

In this study, we propose a broad-scale connectivity map of the freshwater habitats of Europe as a step towards developing a global management plan for freshwater ecosystems. Specifically, we advance on the identification of potentially relevant areas for dispersal-mediated mechanisms that enhance freshwater biodiversity through the ecoregions of Europe defined by Abell et al. (2008). To this aim, we first estimated the areas of ephemeral, temporal and permanent freshwaters for 10×10 km cells across Europe (totalizing 134,244 cells). Within each of the ecoregions defined by Abell et al. (2008), for Europe ($N=37$), we represent the landscape structure of the three freshwater habitats using a weighted spatial graph. Then, three centrality metrics related to mass effects—out-degree and in-degree centrality—and corridor effects—betweenness centrality—were estimated for each cell, considering the spatial distribution of each freshwater environment independently and combining all freshwater habitats. While many conservation strategies focus on identifying isolated areas based on focal species, our study identified regions based on their role in promoting freshwater connectivity at a continental extent, a useful input for underpinning global and regional conservation planning efforts.

2 | METHODS

The freshwater habitats considered in this study were mapped by the Global Surface Water (Pekel et al., 2016) using Landsat satellite images. From the available data, we used the 'Occurrence' data set, since these maps contain surface water occurrences between 1984 and 2020 with a monthly periodicity and at a 30-m spatial resolution (i.e. pixel). The seasonality of surface water was expressed as a frequency of water in the study time period. That is, 0 represents the total absence of water (i.e. land pixel) and 100 represents a permanent water body that maintained its water status during the entire study period. After downloading the corresponding database, we proceeded to treat, depurate and calculate water surfaces. We used ArcGIS Pro to carry out all the data cartographic management, mostly using ArcToolbox > Spatial Analyst Tools (ESRI, 2020). We extracted and used only the European water bodies. Later, we built a reference grid of 10×10 km cells across the entire continent to calculate the water surface and express it as a percentage in each cell. The coordinates of the centroid of the cells were also retrieved to export the obtained data for the analysis. For each cell of the grid, we obtained its total area and the water surface for each percentage value ranging from 0 to 100. Then, we grouped all the pixels within a cell according to three main categories that define three groups of water habitats: permanent (water surfaces with seasonality from 90 to 100), temporary (water surfaces with seasonality ranging from 10 to 89) and ephemeral (water surfaces with seasonality from 1 to 9). Considering the time span of the database, the ephemeral category included areas that presented water with a frequency less than once a year, the temporal category included areas with water frequencies close to once per year on average, and the permanent water category included areas that presented water most of the time. These thresholds provide a proxy of landscape configuration for three main freshwater habitats that although sharing some generalist species, represent three markedly different systems in terms of specific diversity and functioning (Biggs et al., 2017; Kelly-Quinn et al., 2017; Williams et al., 2020). Each of these three categories was mapped individually to assess its distribution across the continent.

We followed the ecoregionalization proposed by Abell et al. (2008) for the world, to define the study units. Although Abell's ecoregions are based on major basins of the world, and biogeographic patterns of fishes, their defined units comprise one or more freshwater environments (not only rivers) and are representative of the biogeography of fishes, but also of other aquatic organisms (see Abell et al., 2008). Then, the waterscape structure was represented by a weighted and directed graph for each freshwater European ecoregion ($N=36$). The nodes of the graph were the 10×10 km cells previously estimated. The weights of the links connecting each pair of cells were estimated as a function of the proportion of potential dispersal between communities, following the incidence function of Hanski (1999):

$$w_{ij} = J_j \bullet \exp^{-b \bullet d_{ij}}, \tag{1}$$

where w_{ij} is the directed link from cell j to cell i; d_{ij} is the geographic distance between communities in kilometres; b is a parameter that captures the decay in dispersal with distance, $b = -\log(0.5)/d_{50}$ with d_{50} being the Euclidean distance between centroids of neighbouring cells at which dispersal decays to half its maximum value. We defined d_{50} as 4 km to represent neighbour cell migration, following Worm and Tittensor (2018); J_j is a proxy of community size in a source cell, and was defined as a function of the freshwater area occupied in that cell, A_j—i.e., $J_j = \left(J_{\max} / A^{0.5}_{\max} \right) \times A^{0.5}_j$, where $J_{\max} = 400$ and $A_{\max} = 100$. This function accounts for the recognition that the population size increases slower than linearly with patch area, perhaps because large patches include unsuitable habitat (Hanski et al., 1996; see also Ritchie, 2010). Following Hanski et al. (1996), the exponent of 0.5 was selected for simplicity and coherence with empirical observations. Finally, it should be noted that the $J_{\max}$ value affects the normalization constant but not the scaling in community density. As a consequence, the selected value for $J_{\max}$ does not has a large effect on the relative centrality estimated for different areas.

Once the weighted graph was defined, three centrality metrics were estimated for each cell (node). The metric 'out-degree' that reflects the potential of a node (local communities) to operate as a source community is the sum of link weights along all the links that start on the reference cell (Newman, 2018). The metric 'in-degree', which reflects the importance of incoming dispersal from other communities for local diversity, is estimated as the sum of all links arriving at the reference cell (Newman, 2018). Additionally, local communities' importance for connecting other communities (corridor effects) is captured by the graph centrality metric 'betweenness'. This metric indicates the number of pairs of other communities that pass through this community in the shortest path that connects them. In-degree, out-degree and betweenness were estimated for each of the 134,244 spatial cells of Europe. All the analyses were performed for all freshwaters combined and for ephemeral, temporal and permanent freshwaters independently, considering the different freshwater ecoregions.

Then, we estimated the log-ratio of each centrality metric (Centrality_{LR}) between each pair of water habitat (i.e. permanent vs. temporary, permanent vs. ephemeral and temporary vs. ephemeral) as an index of the relative importance of the potential routes of dispersal between different habitats—e.g. $\text{Betweenness}_{LR} = \log_{10}(\text{Betweenness}_{\text{temporal}}/\text{Betweenness}_{\text{permanent}})$ (see Riibak et al., 2017 for a log-ratio-based analysis). To this aim, the centrality metrics were standardized between 0 and 1 within each freshwater ecoregion to make them directly comparable. Large positive or negative log-ratios indicate that one specific area could be more important in promoting freshwater connectivity for one type of freshwater habitat than for other. Log ratios close to zero indicate that both areas are similarly important for the connectivity of the two compared habitats. For the log-ratio estimations, only cells that had at least two types of water habitats were included.

3 | RESULTS

The three-centrality metrics pointed to a large-scale structure of the connectivity patterns of the European waterscape (Figure 2). Out-degree centrality identified regions with the potential for acting as sources of individuals to other communities (Figure 2 first map). These hotspots for mass effects were distributed across all ecoregions of Europe. Specifically, Northern and Scandinavian ecoregions (i.e. Norwegian Sea Drainages, Northern Baltic Drainages, Barents Sea Drainages, Southern Baltic Lowlands, Lake Onega–Lake Ladoga) had a big concentration of mass-effect hotspots linked to the overall greater abundance of lentic freshwater and their bigger size, which acted as an important regional source for these ecoregions. Towards southern ecoregions (i.e. Central and Western Europe, Upper Danube, Dniester–Lower Danube and Dnieper–South Bug), the role of great European rivers as main mass-effect hotspots marked a change in regional landscape connectivity, because therein lotic systems are the main hotspots. Finally, in the southernmost ecoregions (e.g. Eastern Iberia, Southern Iberia, Northern Anatolia, Central Anatolia) we observed a mixed connectivity pattern with both rivers (e.g. Ebro River or Kızılırmak River) and lentic systems (e.g. Lake Tuz or Doñana national park area) having important connectivity roles in their ecoregions. Complementarily, in-degree centrality detected a large extension of sink regions, that is areas that receive incoming dispersal from other communities, that could lose a large fraction of their diversity in the case of flow interruption (Figure 2 second map). Here, the previous patterns were mirrored but with a more diffuse distribution, indicating that sink areas were not as concentrated as source areas. For example, main rivers in Central and Western Europe were less relevant as sink areas in most of their regions. On the other hand, coastal regions in the Adriatic and Mediterranean seas (i.e. Dalmatia, Southeast Adriatic Drainages, Ionian Drainages, Vardar, Thrace, Italian Peninsula and Islands, Cantabric Coast–Languedoc) appeared as strong sink areas. Finally, betweenness centrality identified priority communities that composed the potential ecological corridors and were located across all the ecoregions (Figure 2 third map). This facet of the European connectivity was clearly linked to the main rivers along practically all the ecoregions as they constitute the areas where all freshwater paths meet.

When we focussed on each one of the water habitats (i.e. permanent, temporary and ephemeral), we saw changes in their individual contribution to overall connectivity of ecoregions and specially along the latitudinal gradient (Figure 3; Table S1). Permanent water source hotspots were mostly located in northern ecoregions (e.g. Scandinavia and the Lake Onega–Lake Ladoga) but also along some coastal or downstream areas (e.g. Rhine delta in Central Europe ecoregion or the French Mediterranean coast in the Cantabrian Coast–Languedoc). Furthermore, we observed similar hotspot patterns, although more diffused and

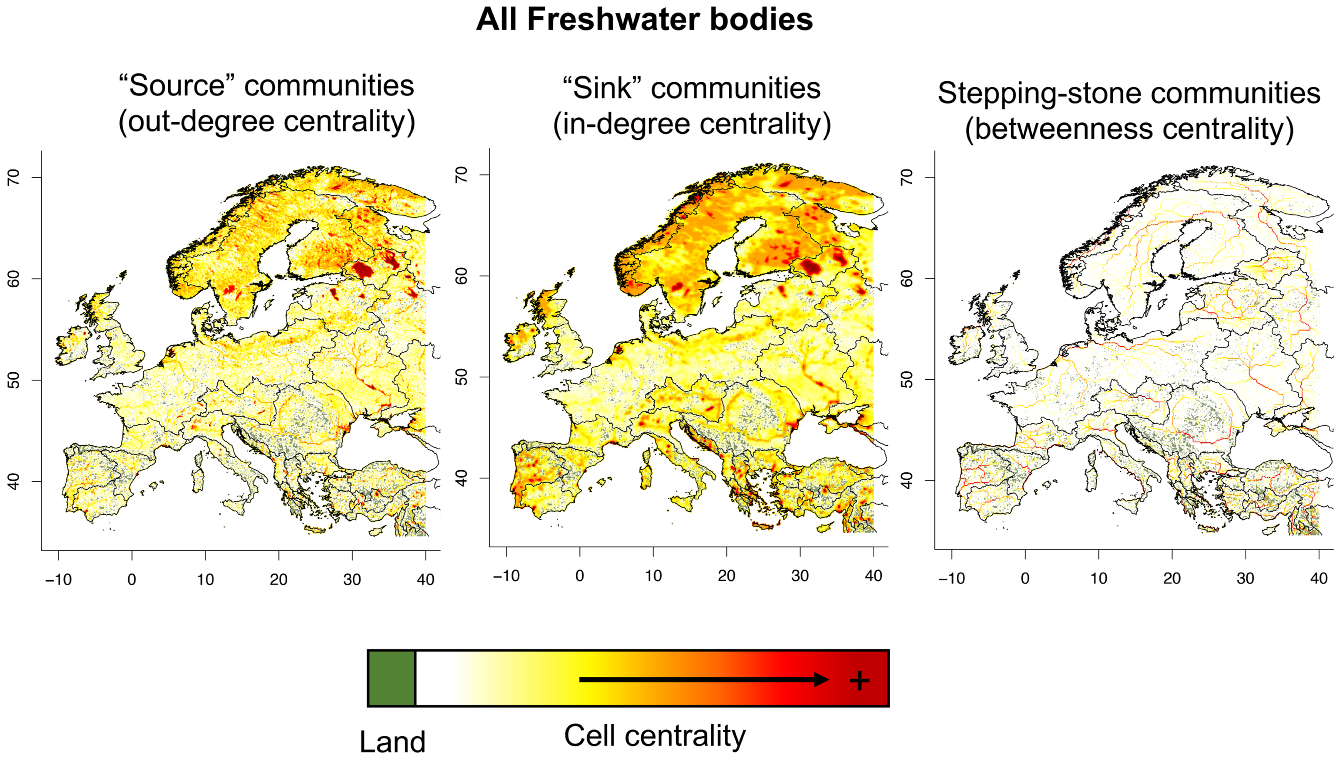

FIGURE 2 Spatial distribution of the centrality metrics that represent the importance of mass effects—source (out-degree) or sink (in-degree) communities—and corridor effects along all freshwater environments. Colours range from yellow to red to indicate increasing values of centrality metrics. Land cells are coloured in dark green, representing areas without records of water on satellite images. The limits of freshwater ecoregions (sensu Abell et al., 2008) are delineated in black. The first map corresponds to the out-degree centrality, indicating regions with the potential of acting as sources of individuals to other communities. The second map corresponds to in-degree centrality, indicating a large extension of sink regions that receive an important flow from other communities. The third map corresponds to betweenness centrality, indicating potential corridors among distant communities. Ecoregions and small-scale information will be available in Dryad (http://datadryad.org) or a similar repository (after acceptance).

concentrated in coastal regions (e.g. Norwegian Sea Drainages, Aegean Drainages) for sink communities (Figure 3a second map). Main ecoregion rivers concentrated most of the relevance for betweenness patterns in permanent systems (Figure 3a third map). Contrastingly, temporary waters were ubiquitously relevant along the whole European connectivity landscape and their hotspots for source, sink and stepping-stone communities were widespread (Figure 3b). Interestingly, in all these cases, more headstream or higher-altitude regions were highlighted as source, but also as sink areas (e.g. Gulf of Venice Drainages, Upper Danube, Central and Western European upstream regions; Figure 3b). Finally, ephemeral waters were also largely widespread, but their connectivity hotspots were more concentrated in headstream regions in the north (e.g. Dnieper–South Bug, Northern Baltic Drainages; Figure 3c) or in specific coastal and headstream areas in southern ecoregions (e.g. Southern Iberia, Gulf of Venice Drainages, Thrace, Western Anatolia; Figure 3c). In these southern regions, both sink and source communities were specially concentrated in determined areas, indicating a heterogeneous distribution of connectivity hotspots throughout the European waterscape (Figure 3c).

Finally, the log ratios of the centrality metrics identified spatial areas with high heterogeneity in their potential role connecting different freshwater types, both within and across freshwater ecoregions (Figure 4). For example, when comparing ephemeral and temporary waters (Figure 4 first column), we observed that for most of Europe, temporal waters were greatly contributing to regional connectivity, both for sink and source communities (Figure 4a,b). However, this pattern was reversed in some ecoregions (e.g. Northern British Isles, Northern Baltic Drainages, Southern Baltic Lowlands), for which ephemeral waters appeared more relevant than temporal ones as sink areas. This pattern was similar when comparing both non-permanent habitats (ephemeral and temporary) against permanent habitats (Figure 4 second and third columns). In this case, permanent waters generally played a less important role for the regional connectivity all along Europe both for sink and source communities. However, this role was inverted in southern ecoregions (e.g. Iberian Peninsula ecoregions, Gulf of Venice Drainages, Anatolian peninsula ecoregions, Dalmatia), where particularly permanent waters were gaining more relevance in regional connectivity patterns as source areas (Figure 4b second column). Stepping-stone communities, which represent all main ecoregion rivers, showed specially contrasting values along river fluvial courses. Permanent habitats have more relevance in downstream sections (e.g. Rhine River), while ephemeral and temporary habitats have more relevance in upstream sections (e.g. Tajo River). Overall, this regional heterogeneity highlighted that different landscape areas could be important for the preservation of different freshwater habitats (e.g. more temporal, or more permanent). Despite that, we also observed that several areas were similarly important for the connection of different habitats (Figure 4 light yellow and light turquoise cells).

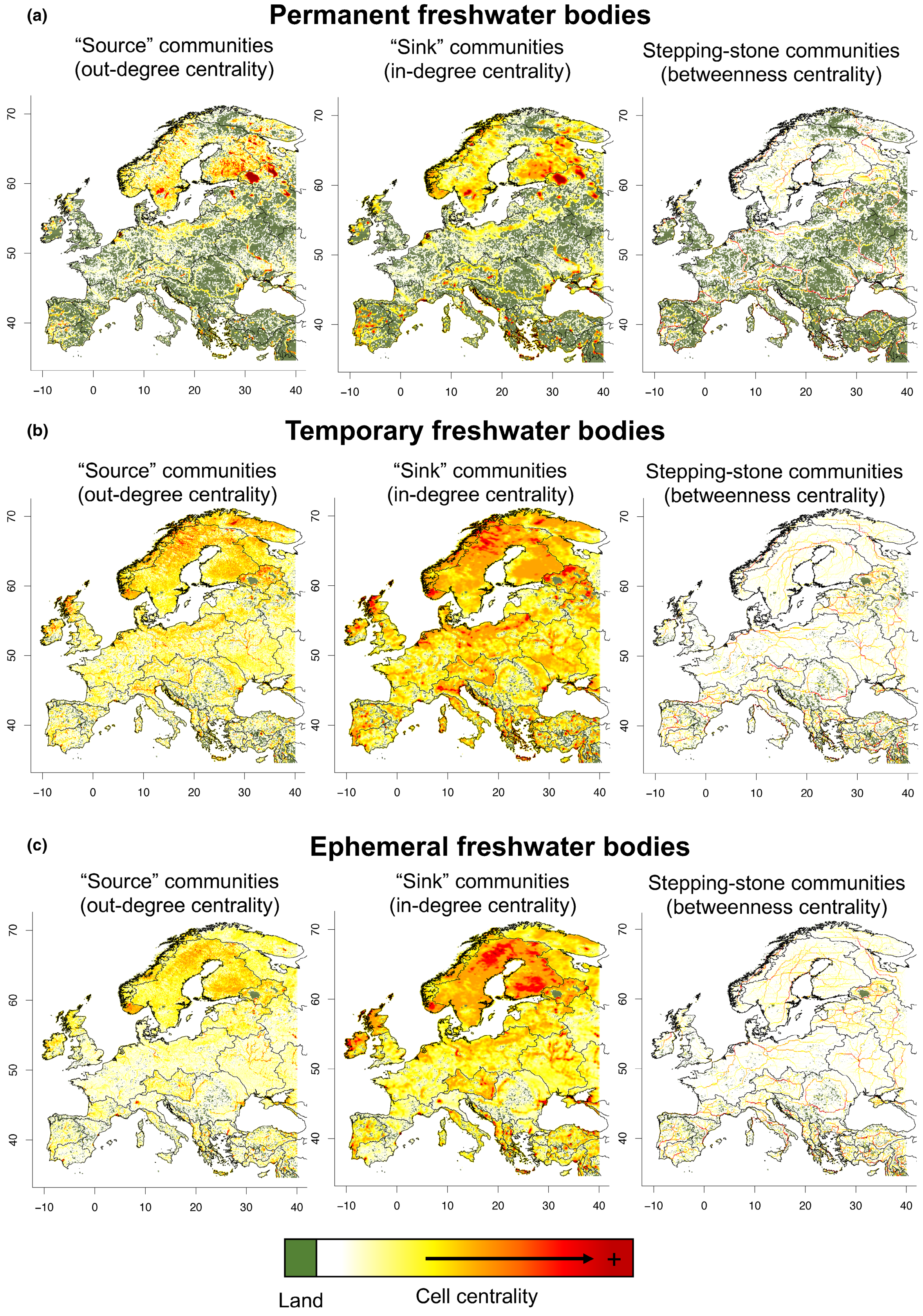

FIGURE 3 Spatial distribution of the centrality metrics that represent the importance of mass effects—source (out-degree) or sink (in-degree) communities—and corridor effects along ephemeral (panel a), temporal (panel b) and permanent (panel c) freshwater environments. Colours range from yellow to red to indicate increasing values of centrality metrics. Land cells are coloured in dark green, representing areas without records of water on satellite images. The limits of freshwater ecoregions (sensu Abell et al., 2008) are delineated in black. The first map corresponds to the out-degree centrality, indicating regions with the potential of acting as sources of individuals to other communities. The second map corresponds to in-degree centrality, indicating a large extension of sink regions that receive an important flow from other communities. The third map corresponds to betweenness centrality, indicating potential corridors among distant communities. Ecoregions and small-scale information can be retrieved at Ecoregions and small-scale information will be available in Dryad (http://datadryad.org) or a similar repository (after acceptance).

4 | DISCUSSION

The spatial structure of the landscape is increasingly recognized as a main determinant of biodiversity patterns and ecosystem functioning (Leibold & Chase, 2018; Préau et al., 2022; Suzuki & Economo, 2021; Wood et al., 2022). The mass effects and corridor effects summarize the functional role of dispersal processes on biodiversity patterns. However, the ranking of different areas from the perspective of their contribution to these processes is a challenge. The recognition of the potential of graph centrality metrics to capture the potential involvement of an area in mass and/or corridor effects is an important step for improving the understanding of metacommunity processes in general and conservation priorities in particular (Carroll et al., 2018; Economo & Keitt, 2010; Haddad et al., 2014; Keitt et al., 1997). With these approaches, we mapped the main features of landscape configuration directly related to metacommunity processes, which are well-connected with diversity and its resilience, that is mass effects and corridor effects (Brown & Kodric-Brown, 1977; Carroll et al., 2018; Haddad et al., 2011, 2014; Leibold & Chase, 2018; Shmida & Wilson, 1985). From these perspectives, freshwater hotspots were estimated for each ecoregion of Europe, showing marked differences along the latitudinal gradient (Pekel et al., 2016; but also see Szabolcs et al., 2022). First, we detected great concentrations of source and sink hotspots areas on the northern regions associated likely to lentic systems. Second, we showed a key role of main European rivers as ecological corridors but differentiated its importance according to their temporal persistence—i.e., permanent, and non-permanent habitats. Third, we identified a mixed and heterogeneous distribution of connectivity hotspots in southern and Mediterranean European ecoregions, likely linked to the presence of water specific areas, either lentic or lotic. Clearly, these patterns alone are not a sufficient criterion on which to base conservation and management decisions. However, the maps presented herein provide important clues about dispersal processes that have been shown to be difficult to infer from other perspectives, for example local studies.

Mass effects were recognized early as a determinant of population persistence and local community diversity (Brown & Kodric-Brown, 1977; MacArthur & Wilson, 1967). Area and isolation were also recognized as the main determinants of the strength of mass effects on community assembly (MacArthur & Wilson, 1967; Zhao et al., 2020). When immigration from neighbouring communities, in addition to the mainland, was recognized to be an important process, the quantification of isolation became a challenge. The incidence function proposed by Hanski (1999) notably captured the combined effect of patch areas and relative location in the landscape on species dispersal (Hanski, 1999). Here, we used the incidence function for the estimation of the links of a spatial network connecting European freshwaters. This network allows further relating of nodes—spatial cells—with sound metacommunity processes. Interestingly, we found that nonpermanent waters could be particularly prominent as hotspot areas of mass effects associated with lentic ecosystems in Northern Europe (e.g. Northern Baltic Drainages and Northern British Isles) or associated with upstream sections of rivers. Especially, temporary habitats are a source for permanent habitats in those ecoregions emphasizing the key role of smaller and less permanent systems as drivers of diversity at regional scales (Bonada et al., 2020; but see also Hermoso et al., 2011). The spatial mapping of hotspot areas for mass effects on diversity dynamics is a promising contribution that can guide management strategies focussed on preserving the spatial processes that determine biodiversity patterns and stability.

Furthermore, betweenness centrality directly estimates how many other communities have to use a given community to maintain a flow of individuals between them, that is the corridor effects (Economo & Keitt, 2010). Betweenness then truly reflects the role of a patch on dispersal through the landscape (Economo & Keitt, 2010; Keitt et al., 1997). Cells with low diversity, low water cover and low apparent importance from a local perspective may be crucial for connecting other regions with higher diversity. This role becomes evident when the spatial network is considered and may be unrelated to the local properties of patches. Our approach captured the main role of rivers as the dispersal backbones of each ecoregion, independently of the latitudinal position, but strongly associated with the main river courses along the European continent. As could be expected, ephemeral and temporary habitats could be more important in upstream sections, while permanent habitats would be more relevant in downstream sections. Such patterns would stress the potential impacts that for example reservoirs have at the regional scale and all along the continent (Belletti et al., 2020), which would cut or diminish the key dispersal paths that bound regional freshwater diversity. The mapping of freshwater hotspot areas for connecting other communities, that is corridor effects, quantifies the potential relevance of these areas for large-scale dispersal from a perspective not evident from local analyses. These corridors frequently span different countries and demand international coordination for their preservation. Corridors and freshwater areas with a disproportionately high role in mass effect dynamics could represent key regions

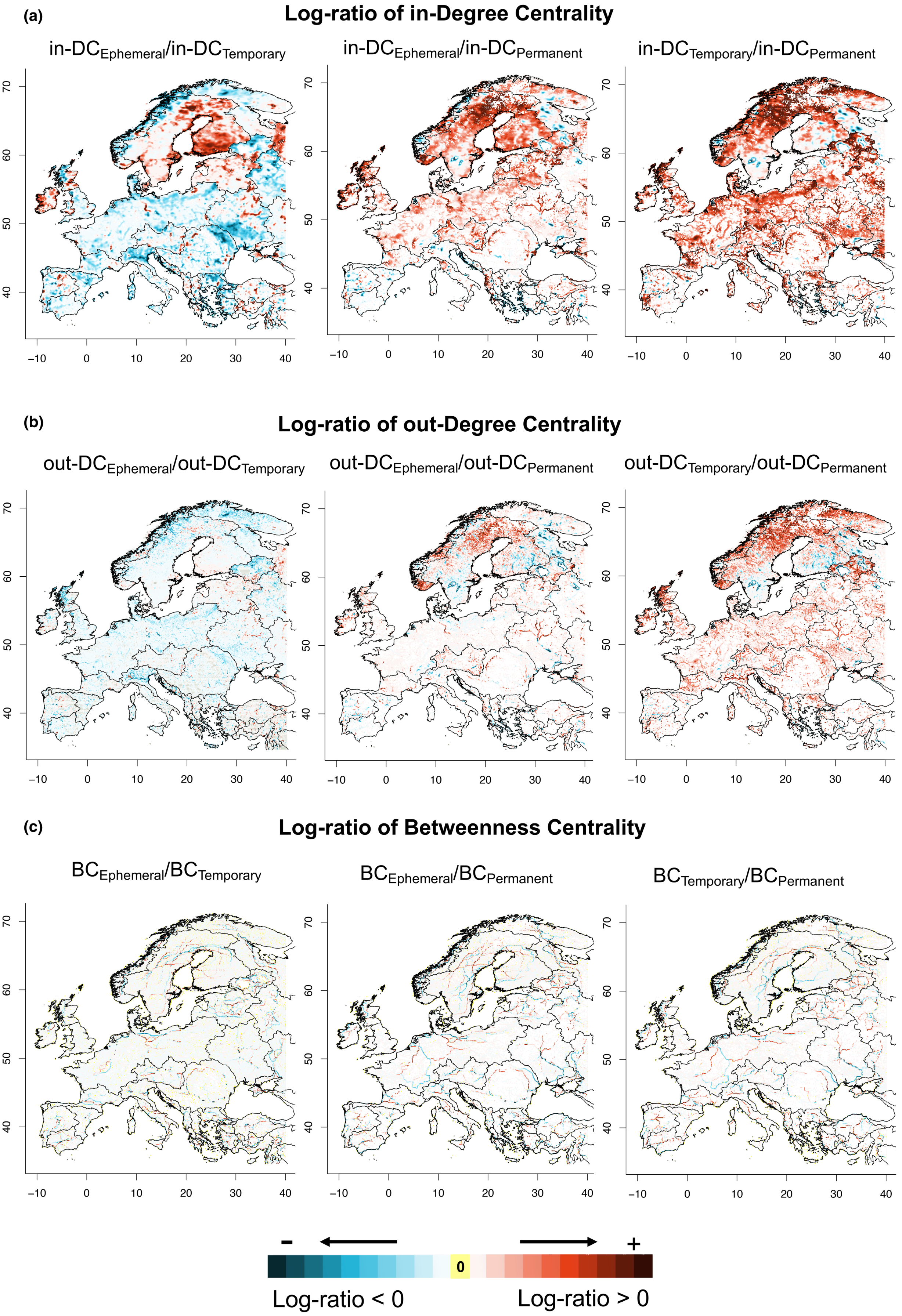
(a)
Log-ratio of in-Degree Centrality
in-DC$_{Ephemeral}$/in-DC$_{Temporary}$
in-DC$_{Ephemeral}$/in-DC$_{Permanent}$
in-DC$_{Temporary}$/in-DC$_{Permanent}$
(b)
Log-ratio of out-Degree Centrality
out-DC$_{Ephemeral}$/out-DC$_{Temporary}$
out-DC$_{Ephemeral}$/out-DC$_{Permanent}$
out-DC$_{Temporary}$/out-DC$_{Permanent}$
(c)
Log-ratio of Betweenness Centrality
BC$_{Ephemeral}$/BC$_{Temporary}$
BC$_{Ephemeral}$/BC$_{Permanent}$
BC$_{Temporary}$/BC$_{Permanent}$
70
60
50
40
−10
0
10
20
30
40
–
+
0
Log-ratio < 0
Log-ratio > 0

FIGURE 4 Spatial distribution of the log-ratio of the out-degree (out-DC_{LR}; panel a), in-degree (in-DC_{LR}; panel b) and betweenness (BC_{LR}; panel c) centralities between two types of freshwater as an index of the relative importance of the potential routes of dispersal. Colours ranging from yellow to red to indicate increasing positive values of log-ratio, while colours ranging from sky blue to dark blue indicate increasing negative values of log-ratio. The black colour corresponds to zero log-ratio values, indicating that both ecosystems could be interchangeable in terms of the connectivity pattern. Cells that do not have the two types of freshwater ecosystems to compare or are land cells are coloured in white. The limits of freshwater ecoregions (sensu Abell et al., 2008) are delineated in black. In each panel, the first map corresponds to the relative importance to connectivity between ephemeral and temporary ecosystems $\log_{10}(\text{Centrality}_{\text{ephemeral}}/\text{Centrality}_{\text{temporary}})$, the second map corresponds to the relative importance between ephemeral and permanent ecosystems $\log_{10}(\text{Centrality}_{\text{ephemeral}}/\text{Centrality}_{\text{permanent}})$, and the third map corresponds to the relative importance between temporary and permanent ecosystems $\log_{10}(\text{Centrality}_{\text{temporary}}/\text{Centrality}_{\text{permanent}})$.

in the waterscape that may disproportionately contribute to landscape diversity. Thus, such regions could be essential for delimiting a network of freshwater corridors and reserves across Europe (Barnett & Belote, 2021).

The spatial structure of the freshwater landscape of ephemeral, temporal or permanent environments clearly differs among the different ecoregions of Europe. For those species that can inhabit all these environments, the waterscape well reflects the spatial network that impacts their diversity. However, species have preferences for specific environments or are even unable to establish viable populations in some environments, for example pond or lake specialists. Indeed, freshwater diversity is composed of a range of species from habitat specialist to generalist that inhabit all environments (Biggs et al., 2017; Kelly-Quinn et al., 2017; Williams et al., 2020). Most freshwater diversity is likely determined by both the specific environment considered—e.g., ephemeral—and its connection with other environments—e.g., temporal, and permanent. Spatial hotspots for mass effects and corridor effects differed along the network of ephemeral, temporal and permanent freshwaters. Preserving dispersal processes in freshwaters may require considering different hotspots for species with different environmental requirements (see Wood et al., 2022), even when the species pools associated with each environment overlap with those of other environments.

The analysis of landscape structure and its effect on dispersal processes at a continental scale is sensitive to several factors that must be explicitly considered (Barnett & Belote, 2021). First, our analyses are based on water cover and its spatial distribution. Differences in land cover and human modification of the environment are not part of the present analyses, but dispersal is known to be affected by them (Barnett & Belote, 2021). It should be noted that the strength of these effects on dispersal are taxa-dependent, and the quantification demands a massive amount of information that is not typically available (Krosby et al., 2015). When the focus is the conservation of specific taxa, the maps or methods provided herein should be combined with existing knowledge about the organisms considered. Graphs might consider links that are directed because of water flow (e.g. Borthagaray et al., 2020) or preponderant winds (e.g. Epele et al., 2021) and the performance of species in each areas be determined by environmental suitability (Borthagaray et al., 2023) determining taxon-dependent dispersal networks (Borthagaray et al., 2015; Cunillera-Montcusí et al., 2021; Keitt et al., 1997; Urban & Keitt, 2001). Second, the scaling in local community size with area depends on the taxonomic and functional groups considered, as well as on the kind of environment analysed (Hanski, 1999; Hanski et al., 1996; Hanski & Ovaskainen, 2000). However, it should be noted that the results regarding the relative values of the out-degree or betweenness of different cells are robust to the assumptions of the scaling exponent. The exception is the unrealistic situation of an exponent close to zero—water cover with the same number of individuals independent of their areas. We used an exponent of 0.5 that is congruent with empirical observations (Hanski, 1999; Hanski et al., 1996). Considering that a narrow range of variation may be expected for this exponent (Hubbell, 2001), the proposed maps are likely robust to this assumption. Third, we considered a continuous dispersal kernel mostly affecting neighbour cells, as this approach has good performance at large geographical scales (Worm & Tittensor, 2018). However, the effect of distance is contingent on the functional group and body size of the species considered (Borthagaray et al., 2012, 2015; Cunillera-Montcusí et al., 2020, 2021; De Bie et al., 2012). This may affect the spatial scale involved in the out-degree and betweenness estimations. However, we found that the spatial distribution of dispersal hotspots was robust to variations in dispersal potential. While this is true at the European scale, at a lower spatial scale, the explicit analysis of a range of dispersal abilities may have to be considered (Borthagaray et al., 2015; Cunillera-Montcusí et al., 2021; Keitt et al., 1997). Finally, in our analysis, it was implicitly assumed that biodiversity-inhabiting cells with large or small water cover values do not vary in composition. This assumption may not be the case, for example, because larger and smaller organisms may demand larger areas to persist (Marquet & Taper, 1998). If diversity composition follows a nested distribution in a range of water covers—composition of poorer areas is subsample of larger areas—the role of hotspots is reinforced. However, if compositional turnover dominates along the gradient of water cover, this should be considered when prioritizing areas for conservation. Having previous considerations in mind, our objective was to provide reference start-up maps for freshwater conservation from a landscape structure perspective. Our analyses capture the potential role of each area in dispersal processes, but diversity is determined by the interaction between dispersal and other processes—speciation-extinction, selection and drift (Vellend et al., 2017).

The results presented in this study provide general messages at the European scale, explicitly mapping the importance of each area for sound metacommunity processes and also detecting areas in which the management of different waterbodies may require alternative strategies. Management of freshwater biodiversity should combine approaches such as the introduced herein with information about other determinants of biodiversity structure and stability. Explicitly, we aimed to identify the real contribution of the study and the mechanisms herein captured; however, we do not promote the use of this method as a black box for guiding management. These are start-up maps for guiding freshwater biodiversity conservation at the European scale that complement empirical and local studies. Areas with the potential to be landscape hotspots may differ among freshwater environments, species functional groups and the metacommunity processes that need to be preserved. Consequently, a pluralistic conception may be adopted, in which different areas may be preserved for different reasons.

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CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted in the absence of commercial or financial relationships that could be construed as a potential conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the Supporting Information of this article. These data were derived from the following resources available in the public domain: https://publications.jrc.ec.europa.eu/repository/handle/JRC109054.

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BIOSKETCH

The co-authors are part of the PONDERFUL Horizon 2020 project. Our aim is to advance the interaction between landscape structure, metacommunity processes, and the structure and function of biodiversity. We attempt to contribute to a mechanistic understanding of biodiversity that supports its management and human well-being.

Author contributions: DC-M, MA and AIB conceived the ideas and designed the methodology; all authors significantly contributed to the study set-up; DC-M and JB collected the data; AIB analysed the data; AIB MA and DC-M lead the writing of the manuscript. All authors contributed to the drafts and give final approval for the publication.

SUPPORTING INFORMATION

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

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