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Dispersal limitation by structures is more important than intermittent drying effects for metacommunity dynamics in a highly fragmented river network

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Abstract: In the Anthropocene, river networks are globally threatened by human activities, creating dramatic consequences for aquatic biodiversity. Permanent and temporary fragmentation by manmade structures and drying events, respectively, are both increasing in rivers worldwide. Although both of these fragmentation types can limit species dispersal, their individual and combined effects in shaping metacommunity dynamics at both local (site-level) and regional (network-level) scales have not been explored. Here, we examined whether processes structuring aquatic invertebrate metacommunities vary through time in response to flow variability in a river network affected by drying and severe fragmentation by manmade structures. We also compared the relative influences of permanent and temporary fragmentation on metacommunity dynamics and hypothesized that permanent fragmentation would be the primary determinant of metacommunity dynamics. We conducted an intensive sampling effort (30 sampling sites × 6 dates) and measured 12 local environmental variables and 4 spatial distances to assess the relative importance of niche- and dispersal-based processes on benthic invertebrate metacommunities across hydrological phases. Spatial distances considered here were overland, network, and 2 fragmentation distances integrating the permanent fragmentation by manmade structures and temporary fragmentation by drying. We used Mantel tests to identify relationships between community dissimilarities and environmental and spatial distance matrices. We identified temporal variability in metacommunity processes with a predominant role of dispersal and no effect of niche-based processes. Metacommunities were shaped primarily by permanent fragmentation, whereas we detected no effect of fragmentation by network-scale drying. Dispersal-based metacommunity processes varied over time, following the wet–dry cycles that characterize dynamic river networks. Our results suggest the importance of key hydrological phases that should be incorporated into conservation perspectives. In addition, we highlight the need to quantify context dependency in metacommunity studies to optimize biodiversity conservation strategies in river-network ecosystems.

Key words: fragmentation, metacommunity, intermittent rivers, temporal variability, manmade structures, drying, benthic invertebrates, dispersal, beta diversity

Ecosystem fragmentation, the division of habitats into smaller and isolated fragments separated by a matrix of human-transformed land cover, is a major threat to biodiversity in the Anthropocene era (Haddad et al. 2015, Crooks et al. 2017). Fragmentation decreases habitat availability and alters dispersal, i.e., the movements of organisms among local habitat patches within ecosystems (Leibold et al. 2004, Brown et al. 2011, Heino et al. 2017). Dispersal interacts with local

environmental selection to play a major role in promoting species coexistence at regional levels (Poff 1997, Leibold et al. 2004, Brown and Swan 2010, Sarremejane et al. 2020). Globally, human activities, including land-use change, dams, and extraction of surface and ground water, are modifying runoff patterns through catchments and altering river flow regimes (de Graaf et al. 2019, Reid et al. 2019). In recent decades, the speed of these changes is unprecedented, accelerating the

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fragmentation and intensity of flow regulation of river networks in most parts of the world (Grill et al. 2019). These alterations threaten freshwater biodiversity, which is experiencing higher extinction rates than in other ecosystems (Reid et al. 2019).

Increased hydropower development in many countries has fragmented river networks through the construction of large and small structures, such as dams, weirs, and culverts (Zarfl et al. 2014). Additionally, the increasing frequency of droughts in recent decades has motivated the development of small water retention structures, which are often located within streams (Habets et al. 2014). These structures include small to very small impoundments with an impounded area $<0.1 \text{ km}^2$ and a volume $<0.2 \text{ hm}^3$ (Lehner et al. 2011). In spite of the low volume of stored water, these impoundments represent 99.5% of the total number of reservoirs worldwide and are the most common anthropogenic fragmentation structures in river networks (Lehner et al. 2011). Together with large dams, they constitute barriers that permanently fragment rivers and, thus, prevent dispersal of organisms within or across networks (Fuller et al. 2015).

Temporary fragmentation of river networks is also becoming increasingly common as a result of natural drying events caused by water abstraction and climate change (Datry et al. 2018, de Graaf et al. 2019). Drying is defined here as the cessation of flow or the complete disappearance of surface water in a given reach (Ruhí et al. 2017). Of the total length of river networks globally, an estimated $\frac{1}{2}$ is prone to drying, and this proportion is increasing in regions experiencing drying trends and over-abstraction (Döll and Schmied 2012). The local effects of drying on aquatic biodiversity are fairly well understood (e.g., Datry et al. 2017), but the effects of drying-induced fragmentation on aquatic biodiversity remain understudied at the network scale for biotic groups, including aquatic invertebrates (but see Cañedo-Argüelles et al. 2015, Crabot et al. 2020, Gauthier et al. 2020, Sarremejane et al. 2020).

Metacommunities, defined as sets of local communities connected by dispersal (Leibold et al. 2004), are also affected by both temporary and permanent fragmentation, which alters the dispersal of organisms among localities (Fagan 2002) and can change metacommunity dynamics (Cañedo-Argüelles et al. 2015). Many studies have used the biogeographical framework of distance decay relationships (Nekola and White 1999) to identify local, niche-based processes as the main determinants of freshwater metacommunity dynamics (Heino et al. 2015). Alternatively, metacommunities in fragmented freshwater systems can be structured by dispersal-based processes (Thrush et al. 2008, Brown et al. 2011, Sarremejane et al. 2017, Gauthier et al. 2020). However, whether this effect of fragmentation is stable or varies over time, notably according to flow variability and wet–dry cycles, remains unknown (Ruhí et al. 2017). During drying periods, local environmental conditions can change dramatically (e.g., increased temperature,

biotic interaction changes, decreased dissolved oxygen), which could favor niche-based processes. In contrast, during rewetting phases, dispersal could become the major determinant of metacommunity structure because of active and passive recolonization (Sarremejane et al. 2017). Characterizing temporal variability in metacommunity processes in river networks prone to drying will promote more efficient monitoring and management of their biodiversity.

The ways in which permanent and temporary fragmentation of river networks jointly shape aquatic metacommunity dynamics may have implications for biodiversity conservation but have not been explored. When manmade structures permanently limit aquatic organisms' dispersal, the effect of drying events on metacommunity dynamics could be reduced because the movement of organisms is already constrained by manmade structures and, thus, temporary dispersal limitation could be undetectable. In contrast, where drying extends over long distances (e.g., several km), dry sections could impose stronger dispersal barriers than manmade structures, particularly for strictly aquatic organisms. Therefore, contextualizing the combined effects of drying with manmade structures on riverine biodiversity is fundamental because focusing on one type of fragmentation or the other could lead to contrasting conservation strategies.

Here, we explored the temporal dynamics of aquatic invertebrate metacommunities in a river network prone to drying and severe fragmentation by manmade structures through the biogeographical distance decay lens. We first hypothesized that processes structuring metacommunity would change within a hydrological year (Fig. 1A). Accordingly, we predicted niche-based processes to be the predominant determinants of metacommunity dynamics during drying periods as shifts from lotic to lentic environmental conditions develop. Conversely, we predicted dispersal-based processes to be predominant upon flow resumption, when organisms recolonize previously dry habitats from perennial refuges in the network. We also hypothesized that permanent fragmentation by manmade structures would be the primary factor determining metacommunity dynamics in this network (Fig. 1B). Accordingly, we predicted stronger relationships between community dissimilarity and physical distances in reaches with only permanent fragmentation (i.e., manmade structures) compared with those including drying events.

METHODS

To test our hypotheses, we coupled an intensive sampling campaign in both time and space to a fine-scale description of permanent and temporary fragmentation patterns in the Thouaret river network, which is a sub-tributary of the Loire river in the Deux-Sèvres department in western France (Fig. 2A). We did this by characterizing environmental variables and sampling benthic invertebrates at river network sites and by

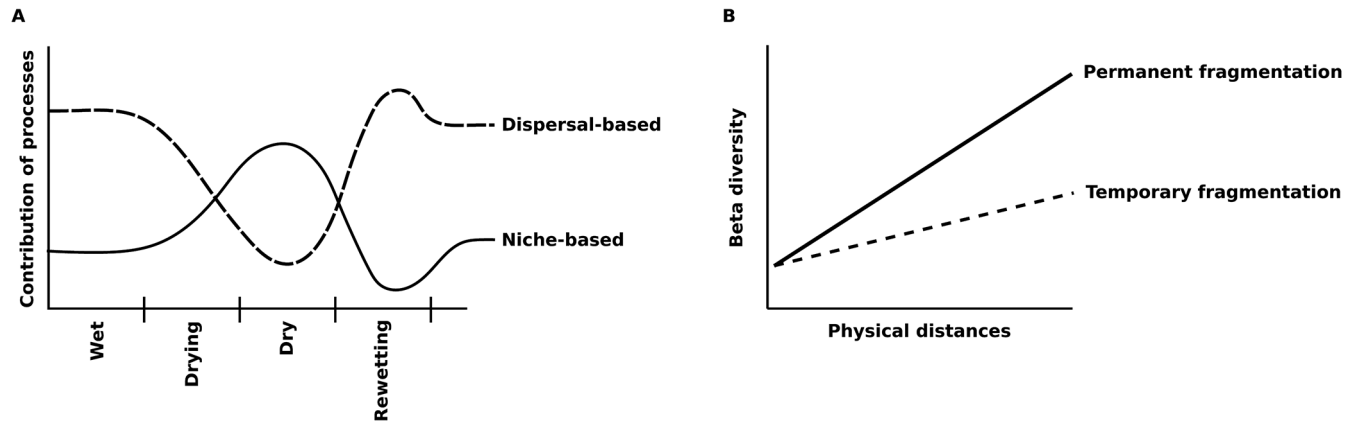


Figure 1. Theoretical contribution of dispersal-based and niche-based processes on metacommunity assembly in fragmented river systems across hydrological phases (A) and expected beta diversity relationships with permanent (i.e., artificial or natural barriers) and temporary (i.e., drying events) fragmentation in such systems (B).

identifying temporary (drying events) and permanent (man-made structures) fragmentation in the river network. We then used Mantel tests to address our 1st hypothesis by investigating metacommunity patterns across hydrological phases. We also used Mantel tests to address our 2nd hypothesis and assess the relative importance of permanent and temporary fragmentation on metacommunity dynamics.

Sampling design

Site selection We selected 30 sampling sites, including sites in 13 perennial and 17 intermittent reaches (Fig. 2B–D), to encompass spatial variability within the Thouaret net-

work and to control for the effects of confluences and man-made structures on community composition. The Thouaret’s hydrological regime reflects the region’s oceanic climate with rainy and cold winters (for the period 1958–2019: mean ±SD cumulative rainfall 233 ± 87 mm, mean temperature 5.2 ± 1.4°C; Vidal et al. 2010) and hot and dry summers (mean cumulative rainfall 135 ± 59 mm, mean temperature 18.0 ± 1.3°C). The impermeable granitic bedrock of the region results in flashy flood events and a lack of baseflow during summer. Hydrological variability is, thus, considerable, ranging between flooding and severe summer low flows and associated drying events (Datry et al. 2016c). The 96-km² Thouaret headwater network drains an area dominated by agriculture

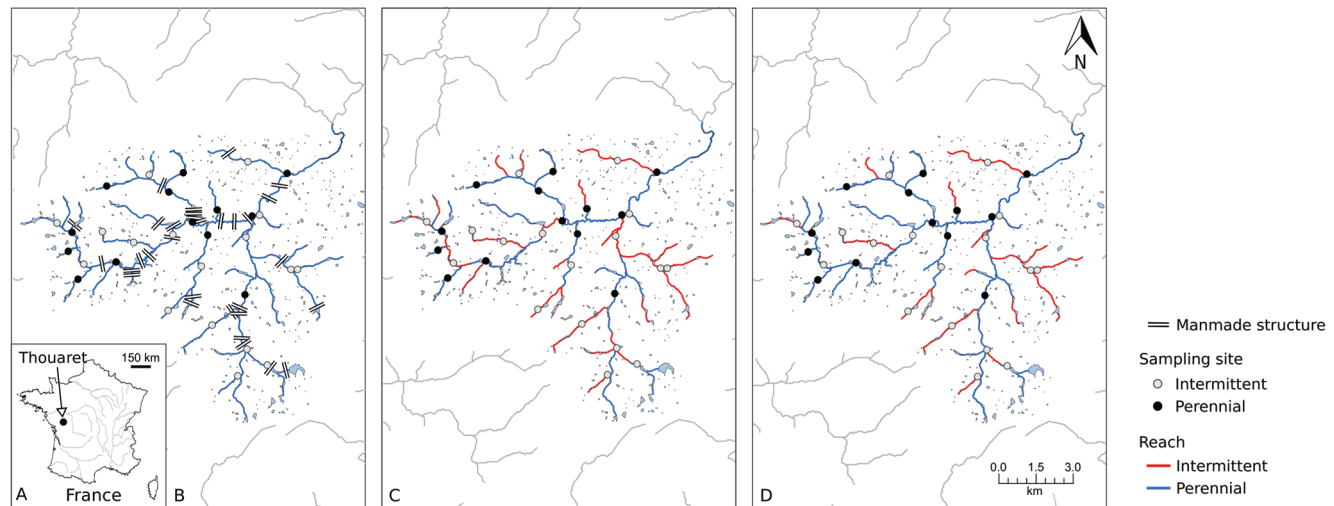


Figure 2. The study river network, the Thouaret, situated in western France (A), during different hydrological phases (B–D), with site locations, manmade structures, and drying patch locations. Hydrological phases for which the entire catchment is flowing (i.e., wet [March, April], drying [June] and rewetting [December]) (B) and the dry phase: September (C) and October (D). Small water retention structures are shown in light blue. Manmade structures are only presented in panel B by black double lines on the network for the sake of clarity.

that includes pasture (35.4%), arable land (28.3%), complex cultivation patterns (23.9%), forest (10%), and urban areas (2.4%). Thousands of small water retention structures have been constructed for agriculture and public water supply in the past decades (exact installation dates are unknown), and some small lentic water bodies along and within the river network are used for recreation and aquaculture activities. These structures permanently fragment the network (Fig. 2B). In addition, dry reaches temporarily fragment the network during low-flow periods between August and October (Fig. 3).

From March to December 2018, we sampled each site 6×, if flowing, to characterize different hydrological phases. One sampling date was during the wet phase in March, 2 dates were during the drying phase in April and June, 2 dates were during the dry phase in September and October, and 1 date was in December during the rewetting phase (Fig. 3).

Characterization of environmental variables We measured 12 environmental variables at each sampling site on each sampling date. At each invertebrate sampling point (see below), we measured water depth (cm), wetted width (cm), flow velocity (cm/s, measured at $0.4\times$ water depth with a Miniwater[®]20 flow meter; Schiltknecht Messtechnik, Gossau, Switzerland), and main and secondary substrate types. We classified substrate type into 14 classes (mud, silt, sand, gravel, pebbles, rocks, slab, litter, root tufts, wood, algae, helophyte, spermaphyte, and bryophyte). We obtained elevation (m), latitude, and longitude at each site with a GPSMAP[®] 62ST handheld navigator (Garmin[®] International, Olathe, Kansas) and measured specific conductivity ($\mu\text{S}/\text{cm}$) and temperature with an HQ14d meter and pH and dissolved oxygen percent-

age with an HQ40d multi meter (Hach[®], Loveland, Colorado). Along an upstream distance of $20\times$ the wetted width of the sampling point, we visually assessed % canopy cover and quantified channel slope with a clinometer. We selected these environmental variables because they are useful in characterizing riffle-associated invertebrate community habitat (Karaouzas et al. 2019).

Benthic invertebrate sampling To address our hypotheses by exploring between-date differences in metacommunity patterns, we sampled organisms from riffle habitat, which is the 1st stream habitat type to dry during drying events (Arscott et al. 2010, Datry et al. 2014, Ruhí et al. 2017, Crabot et al. 2020). This sampling design was validated from a metacommunity perspective through preliminary analysis of 2 other datasets (see Tables S2, S3). We used a Surber sampler (area 0.1 m^2 , mesh size $500\text{ }\mu\text{m}$; Sefar, Switzerland) to collect samples, which we then preserved in 96% ethanol. We counted and identified organisms to the lowest practical taxonomic level with available identification keys (list of references for identification available on Zenodo, <https://doi.org/10.5281/zenodo.3569563>). We identified most insects, crustaceans, triclads, and all mollusks to species except for immature specimens lacking identification features. At a minimum, we identified Diptera to genus, sub-family, or tribe depending on family, Coleoptera, Hemiptera, Trichoptera, and Crustacea (Amphipoda) to genus, and Ostracoda and Copepoda to order. We identified Achaeta and Tricladida to genus and identified Nematoda, Acarina, Hydrozoa, and Oligochaeta to order or sub-order. We assigned each taxon to 1 of 2 dispersal categories according to Tachet et al. (2000):

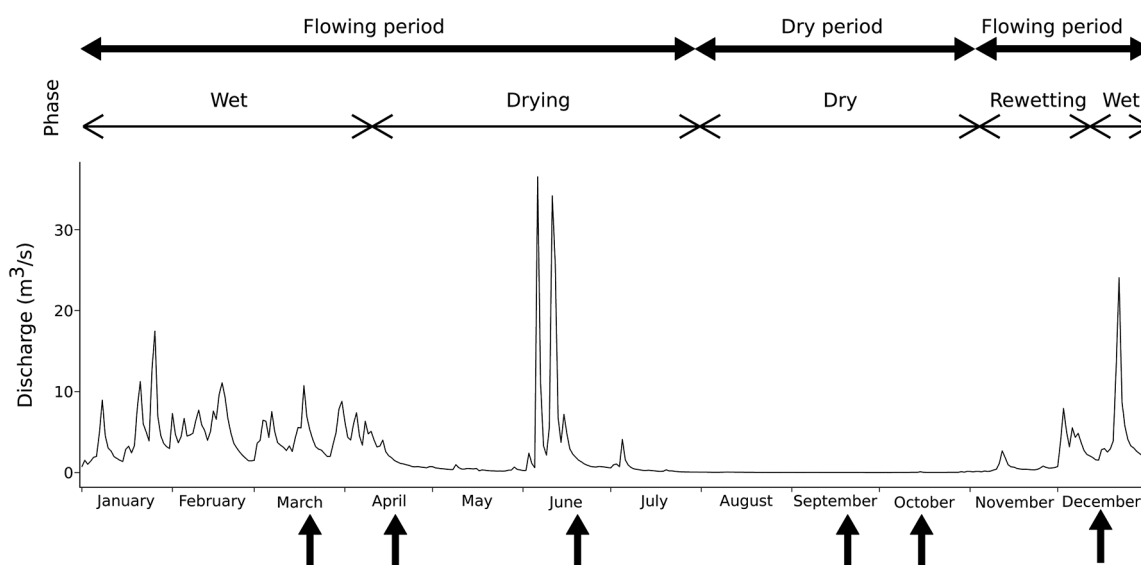


Figure 3. Discharge time series for the year 2018 of a gauging station situated 55 km downstream of the studied Thouaret headwater. Hydrological phases are shown. Sampling dates are represented by vertical black arrows on the x-axis. Data were downloaded from the Hydro database (www.hydro.eaufrance.fr): gauging station L8213010.

1) strictly aquatic invertebrates that can only disperse in water (57 taxa), and 2) those with an aerial life stage (110 taxa), which can also disperse by flying or crawling.

Description of temporary and permanent fragmentation

To identify temporary fragmentation by drying, we quantified drying events by cross-referencing 3 different information sources. First, volunteer members of Carg'eau association (Collectif Associatif Régional pour la Gestion de l'EAU; www.eau-poitou-charentes.org) made visual observations of the Thouaret every 2 wk from June to October of 2018. Observations were classified as 1 of 4 states: 1) flowing, when water flowed across the whole channel width; 2) low flow, when <50% of the reach width was flowing; 3) no flow, when the reach was dry apart from disconnected pools; and 4) dry, when surface water was absent. Observations were made along the entire network whenever possible, depending on accessibility. Datry et al. (2016c) provide a detailed description of the observation methods. Second, within <4 d of the volunteers' observations, we visually assessed the same instream states at each sampling site and along each reach visited during the sampling campaigns. Finally, we installed Hobo® water presence loggers (Onset®, Bourne, Massachusetts) at each sampling site on the streambed in riffle heads. The loggers recorded the presence or absence of surface water every 2 h from March to December 2018. We used this water presence data to calculate the dry duration at each site, defined as the time in seconds without flowing water (i.e., no-flow and dry states). To characterize temporary fragmentation, we calculated the number of dry reaches, the mean and total length of dry reaches, and the percentage of the catchment, as in Datry et al. (2016c). Dry patch delimitations were integrated into a local database based on the larger Carthage network database (<https://geo.data.gouv.fr/fr/datasets/54917fd94fb1cd2fcb6f5d3295dbf33acaf1847e>). To characterize permanent fragmentation by man-made structures, we calculated density (no. of structures/km) and mean structure height for all structures in the network. All measurements related to manmade structures were based on a national Référentiel des Obstacles à l'Écoulement (ROE) database (<http://www.sandre.eaufrance.fr/atlas/srv/ffre/catalog.search#/metadata/59057026-b40c-4cf9-9e3e-7296e0aa1a78>). We used QGIS (v3.10; QGIS Development Team, <https://qgis.org/en/site/>) modules *postres*, *postgis*, and *pgrouting* to calculate all network measurements for both temporary and permanent fragmentation.

Data analysis

Hypothesis 1: Temporal variation of metacommunity processes within a hydrological year To investigate metacommunity patterns across hydrological phases, we used Mantel tests (Legendre and Legendre 2012) to assess the relationships between community beta diversity and environmental and spatial distances between pairwise combinations

of sites on each sampling date. We created beta diversity matrices based on the Chao dissimilarity index to measure dissimilarity after $\log(x + 1)$ transformation of abundance data to better represent rare taxa (Cañedo-Argüelles et al. 2015) with the *vegdist* function in the *vegan* package (Oksanen et al. 2019) in R (version 1.3; R Project for Statistical Computing, Vienna, Austria). For each sampling date, we calculated beta diversity matrices for the whole community and assemblages of taxa in the 2 dispersal categories (i.e., strictly aquatic taxa and taxa with an aerial life stage). To represent niche-based processes, we constructed environmental distance matrices using Euclidean distances based on the 12 environmental variables and the dry duration, after variable standardization (mean \pm 1SD = 0) with *vegdist*. To represent distance-based processes, we assessed 2 spatial distance matrices commonly used in stream metacommunity research (e.g., Sarremejane et al. 2017): an overland matrix based on Euclidean distances constructed from site GPS coordinates with *vegdist*, and a network matrix based on instream distances within the river network constructed using the theoretical hydrographic network described by Pella et al. (2012). For environmental distances, we used the Moran spectral randomization procedure to account for spatial patterns of the environment and to avoid inflation of correlations in Mantel tests (Crabot et al. 2019). We used the Holm correction to adjust *p*-values for multiple comparisons in Mantel tests (Heino and Tolonen 2017).

Hypothesis 2: Effects of permanent and temporary fragmentation on metacommunity structure To assess the importance of both permanent and temporary fragmentation on metacommunity structure, we used Mantel tests to assess relationships between the community dissimilarity matrix described above and 2 fragmentation distances. We used QGIS to calculate a permanent fragmentation matrix by summing the height of manmade structures (ROE database) in meters between pairwise combinations of sites because height can affect the ability of organisms to pass a structure (Fuller et al. 2015). Although this approach did not distinguish the effect of 1 large dam from that of several smaller structures, cumulative height can be more relevant than number of structures when studying network-scale dispersal (Perkin et al. 2015). We also used QGIS to calculate the temporary fragmentation matrix by summing the length in meters of dry patches observed in September between pairwise combinations of sites. We observed the maximum fragmentation by drying in September and, thus, we determined that performing Mantel tests on matrices that included only the final 3 sampling dates was more ecologically meaningful than including all sampling dates. We explored the correlation between the permanent and temporary fragmentation matrices to determine whether to use classic or partial (i.e., correcting for the influence of the other matrix) Mantel tests. We did not find a correlation between

the 2 fragmentation matrices (Mantel test, $r = 0.10$, $p = 0.21$), so we used classic Mantel tests to explore the influence of fragmentation type on community dissimilarities.

RESULTS

Environmental variability

We observed considerable spatial variability in environmental variables on each sampling date (see results in Table 1). The network included sites experiencing a wide range of hydrological conditions, including small and shallow to large and deep reaches (e.g., June wetted widths of 4.7–419.5 cm and depths of 0.6–25.0 cm) as well as standing to fast-flowing conditions (e.g., June flow velocity: 0–0.25 m/s). Physicochemical variables, except for pH, were also spatially variable, and canopy cover encompassed both unshaded and forested reaches. As is typical in riffle habitats, the main substrates were pebbles and gravel, across all sites and dates. The secondary substrate type was mainly composed of gravel, followed by sand and pebbles.

Permanent and temporary fragmentation of the Thouaret network

Both permanent and temporary fragmentation were observed throughout the Thouaret network. We recorded 32 manmade structures, corresponding to a density of 0.37 manmade structures/linear km (Table 2). Dams were the most abundant structures ($n = 15$), supporting water retention for agriculture and aquaculture purpose (60%) and recreation activities (40%). Other manmade structures included weirs ($n = 12$), bridge inverts ($n = 3$), and culverts ($n = 2$). Manmade structure heights ranged from 0.2 to 4.5 m (mean \pm SD: 1.7 ± 1.3 m). We observed temporary fragmentation by dry reaches on both dry-phase sampling dates (September and October; Fig. 2C, D). There were 20 dry reaches in September and 14 in October, with a mean length of 20.6 and 20.3 km, respectively. Dry reaches represented 46.1 and 32.6% of the network in September and October, respectively. Drying duration ranged from 5 h to 3 mo (mean duration: 4.2 wk).

Invertebrate communities

Benthic invertebrate sampling yielded a high number of individuals with similar richness across sites but variable richness over the hydrologic year. We collected a total of 74,337 individuals from 167 taxa with a mean (\pm SD) of 15,723 (± 3188) individuals/date (Table S1) and of 1226 (± 1146) individuals from 19 (± 6) taxa/sample. On average, 58% ($\pm 2.8\%$) of taxa had an aerial stage and 42% ($\pm 2.8\%$) were strictly aquatic. Communities were dominated by Oligochaeta (relative abundance: 32.3%), Tanytarsini (Diptera, 9.1), and Gammaridae (Amphipoda, 8.8%). Oligochaeta was also the most ubiquitous taxon, occurring at 92% of all sites, followed by Orthocladiinae (Diptera, 84.4%) and Tanytarsini (Diptera, 72.5%). Taxa richness was 21.2 (± 5.8) taxa/sample

across all sites and dates (Table S1) and were comparable at intermittent and perennial sites (Student's t -test, $t = -0.006$, $p = 0.99$). Highest average taxa richness was in September (26.9), which corresponded to the dry period when flowing reaches can act as refuges (Bonada et al. 2017) and when density of species is high because of decreased habitat area (Dewson et al. 2007).

Hypothesis 1: Temporal variation of processes influencing metacommunity dynamics

The processes determining aquatic invertebrate metacommunities varied during the hydrological year, supporting our 1st hypothesis; however, our prediction that niche-based processes would dominate during drying periods was not supported. Overland distances were associated with community dissimilarities during the dry phase (mean Mantel's $r = 0.24$, p -value: 0.03–0.04), whereas associations were lower during the rewetting (mean $r = 0.13$, p -value: 0.01–0.04) and wet ($r = 0.12$, p -value = 0.04) phases, and we found no relationships during the drying phase. We detected relationships between community dissimilarities and overland distances for strictly aquatic taxa but not for taxa with an aerial life stage (Fig. 4B, C, Table 3). Community dissimilarities were not associated with environmental or network distances on any date, indicating that, based on the 12 measured variables, niche-based processes were not important determinants of metacommunity dynamics in this network (Fig. 4A–C, Table 3).

Hypothesis 2: Effects of permanent and temporary fragmentation on metacommunity structure

During the dry phase, permanent fragmentation by manmade structures explained more variance in metacommunity structure than temporary fragmentation explained, supporting our 2nd hypothesis. Dissimilarities for the whole community and strictly aquatic taxa were positively correlated with the permanent fragmentation matrix (mean Mantel's $r = 0.20$, p -value: 0.01–0.04; Fig. 5A–C, Table 4). Before the dry phase (March, June), we observed positive relationships between strictly aquatic taxa dissimilarities and permanent fragmentation, suggesting a long-term effect of manmade structures (Table 4). In contrast, taxa with an aerial life stage had no detectable relationships with permanent fragmentation matrices. Community dissimilarities were not correlated with temporary fragmentation matrices.

DISCUSSION

River network fragmentation is one of the most important anthropogenic alterations threatening freshwater biodiversity (Reid et al. 2019). Fragmentation alters the dispersal of organisms within river networks and, thus, has cascading effects on metacommunity dynamics (Gauthier et al. 2020). However, to date, most studies have focused on the effects of permanent fragmentation by manmade structures, whereas

Table 1. Environmental variables measured for each sampling date. Mean (\pm SD) are shown, with the range for each variable (minimum–maximum). Percentage for each substratum type is provided for the main and secondary substrata.

Environmental variable	Sampling Date					
	March	April	June	September	October	December
Elevation (m)			163 \pm 19.2 (126–194)			
Slope (%)			1.3 \pm 0.6 (0.5–3)			
Hydrologic phase	Wet	Drying	Drying	Dry	Dry	Rewetting
Depth (cm)	22.6 \pm 10.7 (5–46)	16.9 \pm 9.8 (4–45)	14.2 \pm 6.1 (0.61–25)	6.0 \pm 2.9 (2–12)	7.0 \pm 3.2 (2–14)	16.4 \pm 8.7 (3–44)
Wetted width (cm)	230.8 \pm 163.6 (51.3–750)	179.7 \pm 117.4 (45.4–429.1)	162.8 \pm 111.5 (4.7–419.5)	116.9 \pm 113.1 (30–457.3)	118.1 \pm 104.5 (30.1–424.1)	191.2 \pm 128.9 (30.1–532.3)
Flow velocity (m/s)	0.44 \pm 0.19 (0.21–0.8)	0.4 \pm 0.26 (0.1–1.22)	0.43 \pm 0.19 (0.11–0.72)	0.1 \pm 0.08 (0–0.25)	0.19 \pm 0.15 (0.03–0.66)	0.56 \pm 0.31 (0.02–1.15)
Temperature (°C)	9.9 \pm 1.2 (7.1–11.3)	13.7 \pm 2.5 (9–17.7)	18.9 \pm 1.2 (16.3–20.7)	17.0 \pm 0.9 (15.8–19)	14.2 \pm 1.2 (12.4–16.6)	7.3 \pm 0.7 (6–8.2)
Conductance (μ S/cm)	225.9 \pm 55.6 (96.3–366)	230.6 \pm 41.5 (116.5–338)	245.2 \pm 46.6 (177.6–373)	333.2 \pm 129.2 (183.2–685)	347.0 \pm 96.4 (192.8–537)	271.8 \pm 76.7 (32.5–476)
Dissolved oxygen (%)	94.2 \pm 6.3 (83.5–108.8)	87.9 \pm 18.4 (10.26–102.9)	82.8 \pm 7.8 (64.8–97.2)	43.5 \pm 28.9 (0.6–89.1)	53.2 \pm 22.5 (1.5–87.4)	88.3 \pm 6.9 (62.3–96.6)
pH	7.42 \pm 0.31 (6.81–8.18)	7.47 \pm 0.22 (6.91–7.76)	7.5 \pm 0.45 (6.86–8.5)	7.42 \pm 0.17 (7.09–7.71)	7.17 \pm 0.26 (6.39–7.61)	7.29 \pm 0.31 (6.67–8.01)
Canopy cover (%)	0–25 to 25–50	0–25 to 25–50	0–25 to 75–100	25–50 to 75–100	0–25 to 75–100	0–25 to 75–100
Main substratum type (%)	Pebbles 53.6 Gravels 28.6 Sand 10.7 Slab 3.6 Mud 3.6	Pebbles 53.3 Gravels 33.3 Sand 3.3 Mud 3.3 Helophytes 3.3 Litter 3.3	Pebbles 53.3 Gravels 30 Sand 6.7 Mud 6.7 Helophytes 3.3	Pebbles 46.7 Gravels 26.7 Mud 13.3 Litter 6.7 Sand 6.7	Pebbles 40.9 Gravels 31.8 Mud 9.1 Sand 9.1 Silt 4.5 Litter 4.5	Pebbles 46.7 Gravels 23.3 Wood 13.3 Helophytes 6.7 Slab 6.7 Sand 3.3
Secondary substratum type (%)	Gravels 51.9 Sand 14.8 Helophytes 7.4 Wood 7.4 Mud 7.4 Algae 3.7 Root tufts 3.7 Slab 3.7	Gravels 56.7 Sand 20 Pebbles 13.3 Mud 10 Helophytes 7.4	Gravels 76.7 Pebbles 10 Root tufts 6.7 Bryophytes 3.3 Wood 3.3	Gravels 73.3 Sand 13.3 Pebbles 6.7 Wood 6.7	Gravels 54.5 Sand 18.2 Pebbles 13.6 Mud 4.5 Silt 4.5 Litter 4.5	Gravels 53.3 Sand 30 Wood 10 Mud 3.3 Spermaphytes 3.3

Table 2. Descriptors of permanent and temporary fragmentation in the Thouaret network. For the temporary fragmentation, values for both dry phase sampling dates are provided. SD = standard deviation.

Fragmentation type	Variables	Value	
Permanent (manmade structures)	Number of structures	32	
	Density (number of structures/linear km)	0.37	
	Mean height of structures (m)	1.69 (± 1.34 SD)	
Temporary (dry reaches)		September	October
	Number of dry patches	20	14
	Average length of dry patch (km)	20.57	20.34
	Total length of dry reaches (km)	40.69	28.80
	Percentage of the catchment (%)	46.09	32.63

the consequences of temporary fragmentation of river networks by drying have only recently been explored (Sarremejane et al. 2017, Gauthier et al. 2020). These recent studies suggest that the temporary fragmentation of river networks leads to shifts in metacommunity processes over time. By repeatedly quantifying the associations between metacommunity and fragmentation patterns in a river network affected by both permanent and temporary fragmentation, our results confirmed that metacommunity processes can greatly vary over time, following wet–dry cycles and temporary fragmentation patterns at the network scale. We found that fragmentation by drying had little effect on metacommunity dynamics within a network subject to considerable permanent fragmentation by manmade structures, indicating that contextualization of the effects of fragmentation by drying is critical to protect and conserve biodiversity of river networks in the Anthropocene.

As we hypothesized, processes structuring the invertebrate metacommunity varied through time across hydro-

logical phases. This finding echoes recent conceptual (Datry et al. 2016a), empirical (Sarremejane et al. 2017), and methodological (Jabot et al. 2020) calls to incorporate temporal variability into the metacommunity framework. These studies also suggested that the relative importance of local and regional processes structuring metacommunities in dynamic river networks could vary substantially over time. Our metacommunity study, which, to our knowledge, is the 1st to describe the physical and biological model of a river network across multiple hydrological phases at such a fine spatiotemporal scale, confirmed that the relative roles of niche-based and dispersal-based metacommunity processes change over time. We suggest that this conclusion may apply to other dynamic freshwater, terrestrial, and marine ecosystems (e.g., Gerisch 2014, Dell et al. 2019).

Although the processes structuring metacommunities varied over time, our conceptual model predicting shifts between local niche-based processes and regional dispersal-based processes was only partially validated. First, we expected

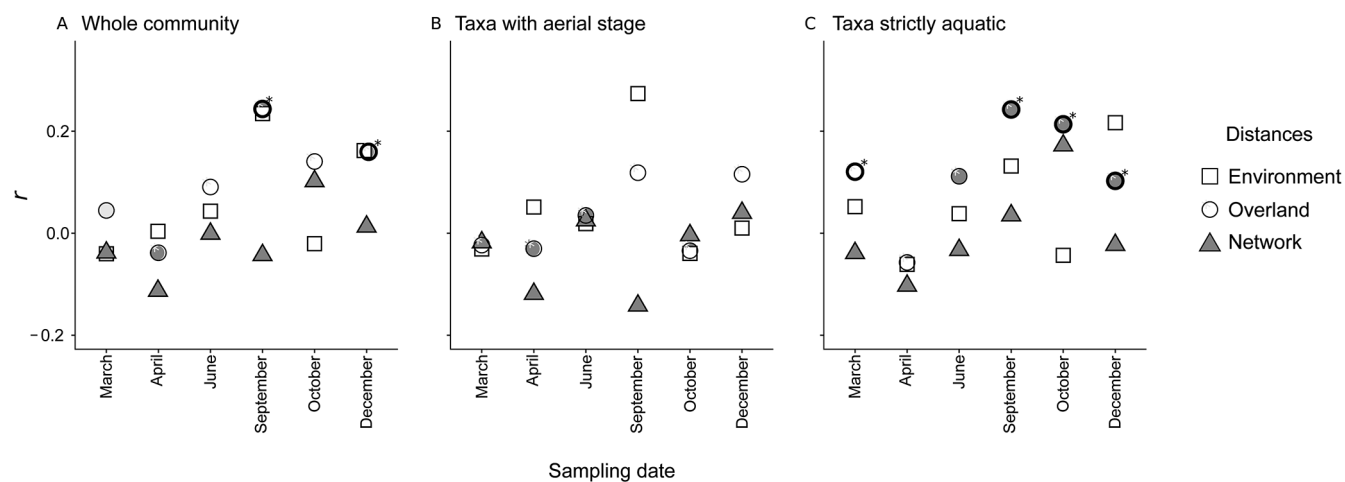


Figure 4. Strength of the relationships (i.e., Mantel's r -values) between community dissimilarities and typical distances (environmental, overland, and network distances) used in metacommunity studies through the different sampling dates for the whole community (A), the community of taxa with aerial life stage (B), and strictly aquatic taxa (C). Relationships with p -values < 0.05 are shown with thicker outlines and an asterisk. r -values of all Mantel tests are available in Table 3.

Table 3. r -values from Mantel tests based on Chao dissimilarity index and typical distances used in metacommunity studies. Distances: Envi = environmental, Over = overland, Netw = network. Relationships with p -values <0.05 are shown in bold.

Sampling date (hydrologic phase)	Distance	Whole community (r)	Taxa with aerial life stage (r)	Taxa strictly aquatic (r)
March (wet)	Envi	-0.04	-0.03	0.05
	Over	0.05	-0.02	0.12
	Netw	-0.04	-0.02	-0.04
April (drying)	Envi	0.00	0.05	-0.06
	Over	-0.04	-0.03	-0.05
	Netw	-0.11	-0.12	-0.10
June (drying)	Envi	0.04	0.02	0.04
	Over	0.10	0.04	0.12
	Netw	0.00	0.03	-0.03
September (dry)	Envi	0.24	0.28	0.13
	Over	0.25	0.12	0.25
	Netw	-0.04	-0.14	0.04
October (dry)	Envi	-0.02	-0.04	-0.04
	Over	0.14	-0.03	0.22
	Netw	0.10	0.00	0.18
December (rewetting)	Envi	0.18	0.01	0.22
	Over	0.16	0.12	0.10
	Netw	0.01	0.04	-0.02

niche-based processes, as defined by the 12 locally measured environmental variables, to be influential during drying, when temperature, nutrient levels, and interspecific competition typically increase and when dissolved oxygen can dramatically decrease (Datry et al. 2016a). However, these environmental variables were not associated with metacommunity structures during any hydrological phase, indicating that niche-based processes were not associated with metacommunity dynamics. In the Thouaret network, although environmental variables varied substantially in space, they did not vary considerably between sampling dates and may not have reached ecologically relevant thresholds. For example, during the drying phase, recorded temperatures did not exceed 20.7°C at any site, which is far below the thermal threshold of most aquatic invertebrates (Quinn et al. 1994). Also, we sampled riffle habitat, but we did not sample pool habitat, which could experience greater change in physicochemical conditions during drying. Including pool habitat may have allowed us to detect a stronger role of niche-based processes. However, the limited influence of niche-based processes on riffle communities in this fragmented river network suggests that metacommunities in intermittent river networks may predominantly be controlled by dispersal. However, many aquatic taxa have adaptations promoting resistance to drying, including the production of desiccation-tolerant, dormant life stages (e.g., Stubbington and Datry 2013), and these adaptations may also partly explain the absence of relationships with local environmental conditions in this net-

work. Such strategies are conceptualized as enabling ‘temporal dispersal’ in metacommunities (e.g., Datry et al. 2016b, Wisnoski et al. 2019) because they promote the persistence of some species in local communities through time, regardless of whether the local environmental conditions define their preferred niche.

We expected niche-based processes to influence invertebrate metacommunity structure during drying phases; however, our result that dispersal was the main process structuring metacommunities in the Thouaret network, independent of hydrological phase, supports other recent studies proposing that metacommunities in dynamic river ecosystems are primarily structured by dispersal (Sarremejane et al. 2017, Gauthier et al. 2020). In intermittent river networks such as the Thouaret, aquatic communities experience local wet-dry cycles, which involve repeated extinction and recolonization events (Datry et al. 2016a). At the river network scale, recurrent recolonization through active and passive dispersal from nearby refuges is a major influence on the organization of biodiversity in space and time (Crabot et al. 2020). Indeed, in our study, community dissimilarities were exclusively explained by physical, overland distances on 4/6 sampling dates. However, these distances only explained a small proportion of total variation, which may reflect ecological drift (Silva et al. 2015), unmeasured environmental factors (e.g., pollutants; Jacobsen 1998), or fragmentation (see below).

In the Thouaret network, permanent fragmentation had a considerable effect on invertebrate dispersal, whereas the

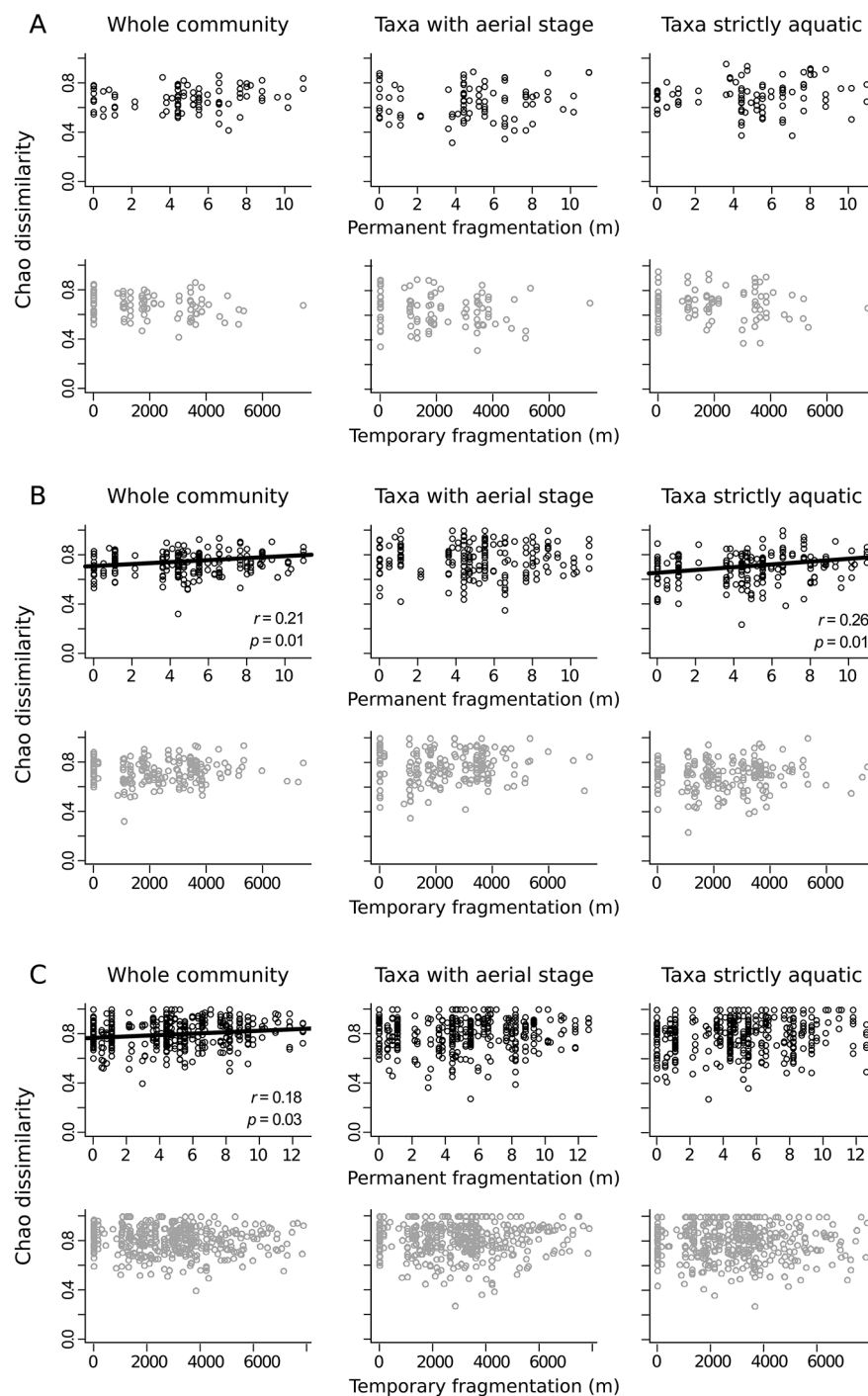


Figure 5. Relationships between community dissimilarities (Chao dissimilarity index) and the 2 fragmentation matrices for September (A), October (B), and December (C) sampling dates and for each community type. Permanent and temporary fragmentation matrices are shown in black and gray circles, respectively. Correspondence of sampling date and hydrological phases: September and October: dry; December: rewetting. Only relationships with p -values < 0.05 are shown with corresponding exact r - and p -values indicated. r -values of all Mantel tests are available in Table 4.

effects of fragmentation by drying were either null or undetectable at the network scale. In contrast, observations by other studies of local-scale differences between perennial and intermittent sites reflect the key role of drying in struc-

turing aquatic communities (e.g., Leigh and Datry 2017, Ruhí et al. 2017), highlighting the effects of drying on riverine biodiversity as context dependent. Additionally, previous studies reporting strong effects of fragmentation by drying on

Table 4. *r*-values from Mantel tests based on Chao dissimilarity index and fragmentation distances used in this study. Perm = permanent fragmentation by manmade structures, Temp = temporary fragmentation by drying. Maximum temporary fragmentation by dry reaches was observed in September, 2018. Relationships with *p*-values <0.05 are shown in bold.

Sampling date (hydrologic phase)	Fragmentation type	Whole community (<i>r</i>)	Taxa with aerial life stage (<i>r</i>)	Taxa strictly aquatic (<i>r</i>)
March (wet)	Perm	0.10	0.05	0.14
	Temp	−0.18	−0.16	−0.13
April (drying)	Perm	0.09	0.07	0.05
	Temp	−0.27	−0.25	−0.21
June (drying)	Perm	0.13	0.07	0.17
	Temp	−0.10	−0.06	−0.12
September (dry)	Perm	0.18	0.00	0.21
	Temp	−0.15	−0.14	−0.07
October (dry)	Perm	0.21	0.062	0.27
	Temp	−0.02	0.01	−0.02
December (rewetting)	Perm	0.18	0.13	0.12
	Temp	−0.13	−0.04	−0.14

metacommunity dynamics were in systems subject to little fragmentation by manmade structures (e.g., Cañedo-Argüelles et al. 2015). In such cases, dry reaches limited aquatic invertebrate dispersal during dry phases, which cascaded through metacommunity dynamics. We found more, and stronger, distance decay relationships between community dissimilarities and physical distances accounting for permanent fragmentation compared with distances including the spatial extent of drying, which suggests that small manmade structures strongly alter invertebrate species dispersal within our river network, as reported for other river metacommunities (Katano et al. 2006, Gauthier et al. 2020) and metapopulations (Blanchet et al. 2010, Taylor et al. 2018). However, the relationships were not very strong, which could be because the high level of fragmentation led to high isolation and, thus, increased ecological drift and species turnover (Merritt et al. 2010).

Context dependency of the effects of river fragmentation were further illustrated by the differential responses to fragmentation by strictly aquatic invertebrate taxa as compared with those that have an aerial life stage, which were much less affected by fragmentation. This partly reflects the highly diverse dispersal modes and capacities of aquatic invertebrates (Heino et al. 2017), which lead to contrasting responses to fragmentation. For example, aquatic invertebrate taxa with an aerial life stage, such as mayflies, caddisflies, and non-biting midges, can colonize previously dry reaches by flying without being severely limited by manmade structures. In contrast, the dispersal of crustaceans, mollusks, and other strictly aquatic taxa was limited, as also has been observed for fishes (Van Looy et al. 2014). In addition to ongoing calls and efforts to better quantify the dispersal routes and capacities of aquatic invertebrates (Downes et al. 2017, Heino et al. 2017), assessing effective dispersal (i.e., dispersal

followed by successful reproduction, ensuring gene flow) by measuring genetic variation among local populations represents the next step toward understanding metacommunity dynamics in fragmented systems and informing conservation plans (Coulon et al. 2010).

Our study, which, to our knowledge, is the 1st to document the effects of both permanent and temporary fragmentation of riverine metacommunities, highlights the need to account for context dependency in metacommunity ecology, particularly for conservation purposes. For example, we observed no additive effects of permanent and temporary fragmentation in any hydrological phases or for any community type (results not shown), which contrasts with other fragmentation contexts in headwater streams of France (Gauthier et al. 2020). Our results also indicate the need to consider the complexity of the effects of drying in river ecology, particularly when exploring network-scale patterns and processes. Further research should explore the synergies and antagonisms between permanent and temporary fragmentation of river networks, which is critical for refining the management and conservation of the rivers of the Anthropocene. This type of study requires substantial effort for extensive field surveys and quantification of biodiversity through sample processing and invertebrate identification, which could present barriers to highly detailed network-scale studies, but novel approaches such as metabarcoding represent opportunities improve the efficiency of research into metacommunity ecology (Bush et al. 2020).

Implications for the management and conservation of river networks

Our results add to recent calls to recognize the temporal variability of metacommunity processes in biodiversity

research toward river conservation (Datry et al. 2016a, Sarremejane et al. 2017, Jabot et al. 2020). That such processes can vary over short timescales in river networks, and most likely in other dynamic ecosystems (e.g., Fernández et al. 2014, Wolkovich et al. 2014), has multiple implications for ecosystem management and conservation planning. For example, assessments of monitoring-site ecological status are mostly based on niche-based processes (Cid et al. 2020), and certain hydrological phases could be more relevant than others for accurate assessments. Identifying such key hydrological phases, as a parallel for keystone species or habitats (Kotliar 2000), will increase understanding of critical metacommunity processes, which will be crucial for improving the success of management practices. Also, conservation actions often need to promote hydrological connectivity during dispersal-limited phases. In cases where fragmentation is mostly due to drying, limiting surface and groundwater abstraction during typically dry summer months could ensure sufficient connectivity for species dispersal within drying river networks (de Graaf et al. 2019).

In the Anthropocene, river networks are experiencing increasing fragmentation by drying events and by the development of small water retention structures for irrigation and human needs (Reid et al. 2019). Previous studies have shown little or no effect of fragmentation by manmade structures on invertebrate communities compared with fish communities (Van Looy et al. 2014, Hwan and Carlson 2016), but our metacommunity approach indicates that small water retention structures can have severe effects on biodiversity patterns. More importantly, the cumulative effects of such structures on riverine biodiversity have not yet been investigated but could be substantial (Linares et al. 2019). As small water retention structures are increasingly promoted as an adaptation strategy to climate change (Habets et al. 2013), we argue that they might considerably alter metacommunity dynamics, resulting in riverine biodiversity loss. Further, determining tipping points of fragmentation levels on metacommunity dynamics is needed to allow prioritization of management efforts, notably with respect to restoration. For example, identifying structure characteristics (e.g., height, passability; Fuller et al. 2015) and their associated effects on metacommunities, as well as determining what fragmentation level is acceptable without altering dispersal among local communities, would be useful for prioritizing geographic locations for restoration and for updating permitting requirements before structures are built. In turn, generating such fragmentation–ecology relationships could reconcile water uses and biodiversity, as well as optimizing the conservation of river networks of the Anthropocene.

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Author contributions: MG, GLF, and BL collected samples. MG, CJD, and TD conceived methodology design. GLF and BL conducted laboratory work. MG and TD conducted data analysis.

MG and TD led the writing of the manuscript, and all authors contributed to writing the manuscript.

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SUPPORTING INFORMATION

Mean value of abundance for each taxon and each sampling date (Table S1), supplementary analyses to test for the reliability of the study sampling design (Tables S2, S3) and outputs of non-parametric permutational multivariate analysis of variances testing differences in community composition between intermittent and perennial sites (Table S4) are available online.

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