

Drying and fragmentation drive the dynamics of resources, consumers and ecosystem functions across aquatic-terrestrial habitats in a river network.

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April 3, 2023

Abstract

Disturbance and connectivity control biodiversity, ecosystem functioning and their interactions across connected aquatic and terrestrial ecosystems, that form a meta-ecosystem. In rivers, detrital organic matter (OM) is transported across terrestrial-aquatic boundaries and along the river network and decomposed on the way by diverse communities of organisms, including microorganisms and invertebrates. Drying naturally fragments most river networks and thereby modify organism dispersal and OM transfers across ecosystems. This may prevent organisms from reaching and consuming OM, generating mismatches between community composition and decomposition. However, little evidence of the effects of drying on river network-scale OM cycling exists. Here, we aim to examine the effects of fragmentation by drying on the structure of consumer communities and ecosystem functioning within interacting aquatic-terrestrial river ecosystems. We monitored leaf resource stocks, invertebrate communities and decomposition rates in the instream and riparian habitats of 20 sites in a river network naturally fragmented by drying. Although instream resource quantity and quality increased with drying severity, decomposition decreased due to changes in invertebrate communities and particularly leaf-decomposer abundance. Invertebrate-driven decomposition peaked at intermediate levels of upstream connectivity, suggesting that intermediate levels of fragmentation can promote the functioning of downstream ecosystems. We found that the variability in community composition was unrelated to variability in decomposition at sites with low connectivity and high drying severity, suggesting that such conditions can promote mismatches between community composition and decomposition. Decomposition instream was correlated to decomposition in the riparian area, revealing one of the first network-scale evidence of the links between ecosystem functions across terrestrial-aquatic boundaries. Our river network-scale study thus demonstrates the paramount effect of drying on the dynamics of resources, communities and ecosystem functioning in river networks, with crucial implications for the adaptive management of river networks and preservation of their functional integrity.

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Key words : subsidies, meta-ecosystems, metacommunities, biodiversity-ecosystem functioning relationships (BEF),

Introduction

Aquatic and terrestrial ecosystems are connected through fluxes of resources (e.g. carbon and nutrients) and organisms, mediated by physical forces (water, wind) and dispersal, as part of a meta-ecosystem (Loreau et al. 2003). River networks are typical meta-ecosystems, in which resources are exchanged across longitudinal (i.e. from headwaters to downstream sections) and lateral (i.e. between riparian and instream habitats) dimensions (Gounand et al. 2018, Harvey et al. 2020, Cid et al. 2022) and transformed by organisms through ecosystem functions such as primary production or decomposition (Hotchkiss et al. 2015, Tieggs et al. 2019). Ecosystem functioning and community composition naturally change along the river network as the basal trophic resource switches from brown – i.e. based on coarse detrital organic matter riparian input – to green – i.e. based on instream algal production – from upstream to downstream (Vannote et al. 1980, Finlay 2001). Although the structuring of resources, communities and their functioning along the river network have been theorized > 40 years ago (Vannote et al. 1980, Gounand et al. 2018), limited empirical evidence of the mechanisms driving such structuring exist, apart from simulations (Jacquet et al. 2022a).

Leaf-litter is a key source of organic carbon and nutrients in rivers, exchanged in both lateral (through leaf fall and runoff) and longitudinal (up to downstream flow) dimensions (Catalàn et al. 2022, Scherer-lorenzen et al. 2022). The decomposition rate of leaf litter in both aquatic and terrestrial habitats depends on several factors including, leaf chemical quality and palatability (Pastor et al. 2014, del Campo et al. 2021a), environmental factors such as humidity and temperature (Tieggs et al. 2019, Annala et al. 2022) and decomposer community (i.e. microorganisms and invertebrates) composition and activity (Abelho and Descals 2019, Boyero et al. 2021). Although leaf-decomposer (shredder) invertebrate communities typically differ between instream and riparian habitats, terrestrial and aquatic decomposers may colonize riverbed and riparian habitats during streambed drying (Corti and Datry 2016) and overbank flooding events (Hutchens and Wallace 2002, Steward et al. 2022), respectively. Thus, lateral movement of consumers could link aquatic and terrestrial exchanges of organic matter (Abelho and Descals 2019, Barthélémy et al. 2022, Scherer-lorenzen et al. 2022), but little evidence of such links exists at the river network scale (Harvey et al. 2020). As a result of decreasing leaf

input from headwaters to mainstem, decomposer abundances and their resource use also typically decrease from up to downstream (Collins et al. 2016, Jacquet et al. 2022a). However, dispersal limitation mechanism preventing species from reaching their favoured habitat or resource because of low connectivity, could lead to sub-optimal functioning in isolated headwaters, despite abundant resources (Leibold et al. 2017, Thompson et al. 2017).

Drying, i.e. the loss of surface water, is one of the most fundamental types of disturbance in river ecosystems, triggering drastic changes in environmental conditions that induce shifts in community composition (Boulton 2003, Datry et al. 2014) and carbon-related biogeochemical processes (Datry et al. 2018). By fragmenting the river continuum, drying can also alter the transport and dispersal of resources and organisms, limiting exchanges between populations (i.e. metapopulations), communities (metacommunities) and ecosystems across the network (Gauthier et al. 2020, Cid et al. 2022). Typically, the diversity and abundance of aquatic organisms such as invertebrates decreases as drying frequency and duration increase (Datry et al. 2014, Soria et al. 2017, Sarremejane et al. 2020) but the colonization of dry riverbeds by terrestrial organisms can counteract those diversity losses (Corti and Datry 2016, Steward et al. 2022). As a result of the negative effect of drying on shredder invertebrates, decomposition rates are usually lower in rivers that experience drying, particularly during their dry phase (Corti et al. 2011) but also during their flowing phase due to legacy effects (Datry et al. 2011, del Campo et al. 2021b). Fungal and bacterial decomposition may however be little affected by drying, if sufficient moisture preserves microbial activity (Riedl et al. 2013, Foulquier et al. 2015). Drying may also affect leaf-litter quality, altering labile carbon contents and nutrient immobilization by microbial communities, which often reduce palatability for invertebrates (Pastor et al. 2014, del Campo et al. 2021a). At least 50% of the world's river networks dry, on average, for one day per year due to geological and/or climatic features (Messenger et al. 2021), and this proportion is likely to increase due to climate change and other anthropogenic alterations (e.g. water abstraction, irrigation; Datry et al. 2023). We urgently need to understand how fragmentation by drying modifies spatial and temporal interactions between organisms and resources at the river meta-ecosystem scale, including across aquatic-terrestrial boundaries (Scherer-lorenzen et al. 2022) to be able to predict when and where adaptive management strategies may be needed to preserve functional river ecosystems under global changes.

Drying and fragmentation may create mismatches between resource and consumer availability if drying and low connectivity prevent efficient aquatic consumers from being present and use resources (Thompson et al. 2017). Such mismatches could result in changes in the biodiversity – ecosystem functioning (BEF) relationship as communities among highly disturbed or isolated environments may not be composed of the most efficient consumers; hence translating into a weak or null BEF relationship across networks fragmented by drying (Brose and Hillebrand 2016, Leibold et al. 2017). However, intermediate levels of disturbances and connectivity may strengthen the BEF by 1) allowing selection of the species best adapted to the environment and resource use and 2) preventing the dominance of functionally inefficient, highly competitive species occurring under low levels of disturbance and high connectivity (Cardinale and Palmer 2002, Leibold et al. 2017).

Here, we aim to examine how resource quality and quantity, the structure of consumer communities and ecosystem functioning respond to drying across lateral and longitudinal dimensions. To do so, we monitored across three seasons leaf resource stocks, invertebrate communities and decomposition rates in the instream and riparian habitats of 20 sites in a river network fragmented by drying. We hypothesize (H1, Fig. 1) that increasing flow intermittence promotes accumulation of leaves of low chemical quality (low conditioning by microorganisms), decreases in invertebrate abundance and diversity and thus lower decomposition rates instream. Instream responses to drying may also change with connectivity and effects may be stronger in less connected headwaters that typically have lower diversity and post-drying recolonization capacity, likely reducing functioning rates there (H2, Fig. 1). Drying may strengthen relationships between instream and riparian resource community and functioning due to homogenization of environmental conditions among these two habitats as the riverbed dries (H3, Fig. 1). Relationship between riparian and instream communities and functioning may also be stronger in isolated headwaters where riparian and instream habitats are more environmentally similar (e.g. shading, moisture) and edge effects more dominant than in more connected

downstream sections (H4; e.g. Harvey et al. 2019). We also hypothesised that the relationship between communities and functioning may weaken with increasing flow intermittence and isolation, potentially driven by mismatches (H5).

Material and Methods

Study sites and environmental conditions

In 2021, we monitored, across three seasons (Spring: March-April; Summer: June-July and Autumn: November-December), 20 sites located in the Albarine river catchment in France (Datry 2012, Gauthier et al. 2020). Although under an oceanic climate, the Albarine is subject to natural flow intermittence due to a permeable karstic bedrock and porous alluvial sediments that induce drying events (lasting from weeks to months) in headwaters and in the main-channel (Fig. S1). The Albarine has a total network length of 150 kilometers of which at least 37% are known to be intermittent (Fig. S1). The riparian zone is dominated by deciduous trees such as ash (*Fraxinus excelsior*) and hazel (*Corylus avellana*), although coniferous trees (e.g. *Picea abies*) can dominate in the upper parts of the river. The 20 sampling sites were selected based on a-priori knowledge of their flow regime in order to represent a gradient of flow intermittence and equal distribution of perennial and intermittent reaches among headwaters and the mainstem (Fig. S1).

Environmental conditions

We estimated the number of dry/ponded and flowing days at each intermittent site, using photo trap cameras, taking twice-daily picture of the river channel. From these pictures we determined the flow permanence (FP; proportion of days flowing during the study period) and the total duration of flowing days during each sampling campaign at each site. We also calculated spatial variables representing site connectivity using geographic information system analyses and digitized network maps that included information on the permanence regime of each reach (i.e. intermittent vs. perennial), based on long-term observations (Datry 2012, Gauthier et al. 2020). To estimate the site location within the network we calculate the distance to the source (DS). We measured distances to the nearest perennial site for intermittent reaches. To estimate upstream connectivity; i.e. the amount of perennial reaches potentially serving as colonization source, we calculated the length, and the percentage of all perennial reaches upstream (%UC) from each site (see e.g. Sarremejane et al. 2017). For graphical representation and analyses, sites were sometimes divided into flow regime categories: perennial (FP = 1; n=10) and intermittent (FP < 1; n=10) and into network location categories: headwaters (DS < 10km, n=14) and mainstem (DS > 10km, n=6).

We also measured a set of environmental variables at each site and in each season. When water was present, pH, conductivity and oxygen concentrations instream were measured using a multiprobe (Hach) and total dissolved nitrogen and soluble reactive phosphorus (SRP) were measured from filtered water samples in the laboratory. Dissolved nitrogen was determined in a TOC-Analyzer with Nitrogen-Analyzer (Shimadzu) and soluble reactive phosphorous (SRP) was determined with the molybdate blue reaction (spectrophotometer U-3900H, Hitachi). Flow velocity was determined using a flowmeter at 10 to 30 (depending on channel width) random locations at each reach. The wetted width was averaged across 10 transects. Instream bryophyte and substrate (bedrock, boulders, cobbles, gravel and sand) cover was determined visually. Riparian soil and instream sediment samples were dried (700C) and burnt (5500C) to ashes in the laboratory to determine moisture and organic matter content, respectively. In summer, we estimated canopy cover in the instream and in the riparian area at each site, using a vertical tube (15 cm diameter) at 10 random locations. We also identified all ligneous plants located in the riparian area (<5m from the stream) and estimated their relative density and the total tree richness at each site. Temperature was recorded hourly for the duration of the study instream and in the riparian area using iButton dataloggers (Maxim Integrated Products, USA). Site altitude above sea level was also determined from a digitized elevation model.

Leaf litter quantity

To estimate leaf-litter standing stocks, we sampled leaf material at 10 random locations using a 0.11 m² quadrat, on the riparian ground (5 on each bank, <1m from the bank top) and on the streambed at each

site and in each season. In riparian habitat and on the streambed when dry, all visible detrital leaf material was hand-picked within the quadrat. In flowing instream habitats, organic matter was collected in a driftnet (mesh size = 500 μm) attached to downstream side of the quadrat, after hand-disturbing the substrate to suspend organic matter in the water column. For each habitat, the 10 samples were combined in the field and taken to the lab where they were rinsed and cleaned from sediment, invertebrates, twigs and rocks. Remaining leaf material was then oven-dried at 70°C for 78h, and weighed to estimate dry mass. A subsample was then burnt at 550°C to estimate ash-free dry mass.

Leaf litter quality

In each campaign, additional leaf material was randomly hand-picked next to each quadrat locations in the riparian and instream area, separately, to estimate overall carbon and nitrogen content of each site's habitat-specific leaf stocks. Samples were preserved in a freezer and random sub-samples (approx., 10% of original sample) were freeze dried for one day, grinded into powder and encapsulated ($0.005\text{g} \pm 10\%$) in tin capsules. Nitrogen (%N) and carbon (%C) concentrations were determined with an elemental analyser (FlashEA 1112 HT, Thermo Electron Corporation), using aspartic acid (C: 36.09%; N: 10.52%) as a calibration standard, and sorghum flour as quality control (C: $41.26\% \pm 0.20$; N: $1.47\% \pm 0.25$).

Leaf litter decomposition

To measure leaf litter decomposition rates, we enclosed $4 \pm 0.05\text{g}$ and $2 \pm 0.05\text{g}$ of dried Alder (*Alnus glutinosa*) leaves in 1 cm mesh (coarse-mesh) and 250 μm mesh (fine-mesh) bags, respectively. Where coarse-mesh bags allowed invertebrate to enter and consume leaves, fine-mesh bags only permitted microorganism-driven (i.e. by fungi and bacteria) decomposition (e.g. Datry et al. 2011, Foulquier et al. 2015). Alder leaves were collected in autumn 2020 from a single site, near Chambéry, France (approx. 80 km from the Albarine), air-dried inside the laboratory and then oven-dried for 48h at 70°C prior to being weighed and enclosed into the bags. Six coarse- and six fine- mesh bags were incubated for 29 ± 4 days (mean \pm SD) in the riparian (n=3 of each mesh-type) and instream (n=3) habitats at each site and campaign.

At the end of the incubation period, bags were taken to the laboratory where remaining leaves were cleaned from sediments and other organic matter (e.g. invertebrates, twigs, other leaves). Remaining leaves were then oven-dried and ashed as described in the “Leaf litter quantity” section. Decomposition rates were calculated for each litter bags based on the negative exponential decay model (K) corrected for the duration of incubation and cumulative temperatures (i.e. degree days; Swan et al. 2021). The decomposition rates were then averaged across the three bags exposed in each habitat (instream vs. riparian) at each site and in each season. Of the total 720 mesh bags incubated in the field nine and four fine-mesh and six and two coarse-mesh bags were lost in the instream and riparian habitats, respectively, due to floods mainly.

Invertebrate community

Aquatic and terrestrial invertebrates (size > 500 μm) present in each coarse-mesh bag were picked, identified under the microscope and counted in the lab. More than 15,000 individuals were found, of which 86% and 14% were dominantly aquatic and terrestrial, respectively. Taxa were mostly identified at genus and family taxonomic levels (Table S1). We calculated taxa richness in each site and campaign as the sum of taxa identified.

We used a fuzzy-coding approach to determine aquatic and terrestrial taxa feeding habits from different bibliographic sources (Table S1). Values of 1 to 3 were given to indicate weak to strong affinity with each feeding category (e.g. leaf-shredder or grazer, Tachet et al. 2010) to account for variability in feeding preferences within taxa (e.g. feeding habits may change during taxon life cycles) and among species within the same taxon. We then transformed this information into percentage affinity for each feeding category. To calculate the abundance of leaf-shredders in each sample we summed the products of each taxon's percentage affinity to the “leaf-shredder” category with its abundance. Trait information was missing for 39 taxa representing 0.2% and 9.1% of the total aquatic and terrestrial individuals, respectively, which were thus not taken into account when calculating leaf-shredder abundances. Most of those individuals (55.7%) were ants,

which have very diverse feeding habits and little impact on leaf litter decomposition. Total taxa richness and leaf-shredder abundances were divided by the number of coarse-mesh bags retrieved in each habitat and campaign to account for bag losses. One site, affected by a scouring flood, was not sampled in summer.

Statistical analyses

Prior to running models and analyses, we used variance inflation factor (VIF) analysis to assess multicollinearity among predictor variables, and sequentially removed those with the highest VIF until all had a $VIF < 3$ (Zuur et al. 2010). Total number of flowing day, distance to the nearest perennial site, and the length of upstream perennial reaches were collinear with other variables and were thus removed from analyses. We also used Pearson’s correlation coefficients to assess correlations between FP and remaining connectivity variables (i.e. DS and %UC). To characterize site environmental conditions we performed a principal component analysis (PCA), including all environmental variables (except FP, DS and %UC) averaged across season for each site. We further used a permutational analyses of variance (PERMANOVA based on Euclidean distance) to assess if environmental characteristics differed among intermittent and perennial sites.

To address H1 and H2, we designed a set of linear mixed effect models (Table 1) to estimate the effects of environmental, hydrological and connectivity variables on the responses of the instream leaf stock quantity (dry mass), leaf litter quality (%N, %C and C/N), invertebrate community structure (taxa richness, and leaf-shredder abundance) and decomposition rates driven by invertebrates (coarse-mesh bags; CK) and microorganisms (fine-mesh bags: FK; Table 1 & S2). To test H3 and H4, in each model, we also included the riparian response (equivalent to instream response; e.g. riparian CK for instream CK) and its interaction with FP and DS as continuous predictor allowing us to assess if relationship between instream and riparian processes changed with flow intermittence and along the river network (Table 1). To test H5, we included either richness or leaf-shredder abundance as predictor and their interaction with FP and DS in CK models only, allowing us to assess if the link between communities and functioning changed with hydrological and spatial variables (Table 1 & S2). Polynomial regressions were in some case attempted, when data exploration revealed clear non-linear relationships.

We used a model-averaging approach to select the most influential set of predictors and to calculate parameter estimates and significance for each response variables. This way, all potential combinations of predictors were assessed but only parameters of models with a Δ Akaike’s information criteria corrected for small-sample sizes (AICc) < 2 from the model with the lowest AICc were selected and their estimates averaged (Anderson 2008). Pseudo Nagelkerke’s R^2 were also calculated to estimate model goodness-of-fit (Nagelkerke 1991) and averaged when more than one model was selected. To account for the non-independence of samples from individual sites, we included site as a random factors in each model. All predictors was centred around their mean and scaled (i.e. divided by their standard deviation). In a few cases, response variables were transformed, and outliers removed (Table 2) to ensure model assumptions of heteroscedasticity and normal distribution of residuals. To reduce the disproportionate effect of a few large DS values, DS was log-transformed in all models.

To address H3 and H4 in greater detail, we used another set of LMM to determine if leaf stock characteristics, community composition and decomposition differed between habitats (riparian vs. instream) and if differences depended on site location (headwater vs. mainstem) and flow regimes (intermittent vs. perennial). In these models, instream and riparian responses were treated together as response variable and the categorical variables habitat, location and flow regime and their interactions were used as predictor. We also calculated pair-wise Euclidean distances between 1) leaf resource characteristics (stock, C/N and %N) and 2) ecosystem functions (CK and FK), and 3) Bray-Curtis dissimilarity between invertebrate communities to assess and visualize differences in resource, functioning and communities among habitats, locations and flow regimes. We used non-metric multidimensional scaling (NMDS) to visualize community variability and PCA ordinations to visualize resource and ecosystem function variability. We used PERMANOVA to further assess if leaf stock characteristics, community composition and decomposition among sites differed depending on their location (headwater vs. mainstem), habitats (riparian vs. instream) and flow regime (intermittent

vs. perennial). We used “season” as a strata argument to constrain permutations among seasons. We used post-hoc tests when interactions between habitat and location or habitat and flow regime were significant to identify which group combinations differed from each other.

To further explore H5 and determine how the relationship between instream invertebrate-driven decomposition (CK) and invertebrate community changes with flow regime and locations we used a Procrustes analysis, comparing the similarity between two matrices in multidimensional space (Peres-Neto and Jackson 2001). For this, we compared the pair-wise Euclidean distance between CK values and the Bray-Curtis community dissimilarity matrix among perennial, intermittent, headwater and mainstem groups, separately.

We used R version 3.5.0 (R Core Team 2018) for all analyses, including the packages *vegan* (Oksanen et al. 2019) for PERMANOVA and Procrustes analyses, *lme4* (Bates et al. 2015) and *MuMIn* (Bartoń 2019) for model building and averaging, *usdm* (Naimi et al. 2014) for VIF analyses.

Results

Site location within the network, i.e. distance to source (DS), was uncorrelated to flow permanence (FP) and upstream connectivity (i.e. the percentage of perennial upstream reaches (%UC)), confirming that perennial and intermittent sites were evenly distributed throughout the river network (Fig S1 & S2). Upstream connectivity was moderately correlated with FP ($r = 0.58$, Fig. S1). Environmental characteristics were similar among intermittent and perennial sites (PERMANOVA: $F = 1.243$, $p = 0.259$; Fig S3) but differed among network locations due to differences in mean wetted width, instream canopy cover, pH, and soil moisture and organic matter contents between headwaters and the mainstem (PERMANOVA: $F = 4.192$, $p = 0.001$; Fig. S4).

Effects of drying and connectivity on instream processes (H1 & H2)

Instream leaf stocks decreased with FP and increased with %UC. The negative effect of FP on instream leaf stock was stronger in autumn than in other campaigns (Table 2, Fig. 2a). Leaf C/N content increased (i.e. quality decreased) with FP (Fig 2b), but mainly so during spring and autumn, while it decreased with DS in spring and summer (Table 2, Fig 2c). %N showed opposite patterns to C/N and likely drove changes in C/N, whereas %C increased with FP and %UC (Table S3). Leaf C/N was lower in summer and autumn than in spring, while leaf stock was higher in autumn than in other seasons (Table 2).

Instream invertebrate richness and leaf-shredder abundance increased with FP (Fig. 2d) and this effect was more pronounced as DS increased particularly for richness (Fig2e) but less so for shredder abundances (Table 2). Shredder abundance also increased with %UC in spring and autumn (Fig 2f), whereas richness decreased with increasing C/N, i.e. as leaf quality decreased (Table 2).

CK increased with FP (Fig. S5) and this effect was mediated through changes in shredder abundances, when those were included in the models (Table 3). CK also increased with UC% and data exploration revealed that an orthogonal quadratic (Table S4) (i.e. bell shaped) regression ($AICc = -510.9$) was a better fit than linear ($AICc = -503.5$), particularly at low DS (i.e. among headwaters; Table S4, Fig 2g). An even better set of models ($AICc = -518.0$), including network location (categorical) as interacting factor with DS (continuous), revealed that CK increased with DS among headwaters only (Fig 2h; Table S4). Decomposition rates in fine mesh bags (FK) increased with DS in summer (Table 3, Fig. 2i) and slightly decreased with leaf-stock quantity.

Relationship between instream and riparian processes H3 & H4.

Leaf stocks were higher, and C/N, shredder abundances, CK and FK lower, in the riparian than in the instream habitat, respectively (Table S5). Invertebrate richness did not differ between the instream and riparian habitats, except at mainstem, where instream richness was higher than riparian richness (Table S5).

The relationships between riparian and instream responses were relatively weak but selected for most of the response variables, apart from C/N (Table 2 & 3). Although invertebrate community responses were weak, instream invertebrate taxa richness tended to decrease and increase with riparian richness at low and

high DS, respectively (Table 2; Fig S6). Contrastingly, instream leaf-shredder abundances increased with increasing riparian abundance, and more so as FP increased (Table 2; Fig S6). Instream CK increased with riparian CK but only among sites with higher DS, i.e. the mainstem (Table 3, Fig. 3a). Instream FK was positively related to riparian FK, particularly in spring and this relationship increased as flow permanence decreased, i.e. among intermittent sites (Table 3, Fig. 3b).

Leaf stock characteristics differed between network locations and habitats (Table 4) and instream vs. riparian leaf stock characteristics tended to be more similar in the mainstem (pairwise PERMANOVA: $F = 3.096$; $p = 0.034$) than in headwaters ($F = 10.788$, $p = 0.001$; Fig. 4a). Invertebrate communities differed among habitats, locations and flow regimes (Table 4); significant interactions indicated that communities differed more among locations and flow regimes instream than in the riparian area (Fig 4b, c). Decomposition differed among flow regimes and habitats (Table 4) with greater differences among flow regimes instream ($F = 12.127$; $p < 0.001$) than in the riparian zone ($F = 0.078$; $p = 0.760$; Fig 4d).

Relationships between instream communities and decomposition (H5)

Shredder abundance had a strong positive effect on instream CK and this effect decreased with increasing DS and UC% (Table 3, Fig. 5). Richness was however not selected among the best predictors when included in similar models. The multivariate variation in community was related with the variability in CK among perennial sites (Procrustes; $r = 0.431$, $p = 0.002$) and headwaters ($r = 0.438$, $p = 0.001$), marginally so for mainstem sites ($r = 0.450$, $p = 0.06$) but not among intermittent sites ($r = 0.286$, $p = 0.121$).

Discussion

Recent microcosm experiments and model simulations have unravelled how lateral (Harvey et al. 2020) and longitudinal (Jacquet et al. 2022a) exchanges of resources can shape network-scale biodiversity and how drying patterns may influence the dynamic of resource processing (Catalàn et al. 2022) and communities (Jacquet et al. 2022b) within river networks. However, comprehensive field-based evidence is missing. Our network-scale field study confirms the paramount effect of drying in governing resource stocks, community composition, ecosystem functioning and their relationships in river meta-ecosystems. As expected in H1, flow intermittence had a positive effect on instream leaf quantity, but a negative effect on shredder abundance and hence on organic matter decomposition rates. Partially agreeing with H2, invertebrate communities and decomposition rates changed throughout the river network in response to upstream connectivity, but not always linearly. Interestingly, invertebrate-driven decomposition peaked at intermediate levels of upstream fragmentation, revealing the potential positive effects of upstream drying on the functioning of downstream ecosystems. Instream and riparian responses were generally weakly related but the relationship between riparian and instream decomposition rates changed with flow permanence (FK; H3) and network location (CK; H4), suggesting that the links between riparian and instream ecosystem functioning can change depending on the disturbance regime and network-scale connectivity. Although invertebrate richness did not directly relate to decomposition, community composition and shredder abundance did, and the strength of these relationships was lower among intermittent and headwater sites (H5), suggesting that flow intermittence and low connectivity may induce mismatches between community composition and ecosystem functioning.

Although the negative effects of flow intermittence on decomposition can be linked to changes in leaf resource nutritional quality (del Campo et al. 2021a), most field studies attribute these negative effects to losses of primary consumers such as shredders (Datry et al. 2011, Schlieff and Mutz 2011, Abril et al. 2015, Northington and Webster 2017). We found that increasing flow intermittence had a seasonal positive effect on instream resource quality and quantity, but the negative effects on invertebrate richness and shredder abundances drove the associated decreases in decomposition. Our results echo those from Catalàn et al. (2022), who demonstrated through simulations that coarse particulate organic matter (e.g. leaves) tend to accumulate and remain unprocessed – thus conserving a higher reactivity – on dry riverbeds. Such accumulation can result from decreases in transport caused by low or null water discharges and the absence or low abundance of efficient decomposers such as aquatic shredders (Northington and Webster 2017). In our study, decomposition was associated to invertebrate community variability among perennial but not intermittent sites, suggesting

that flow intermittence may create mismatches between community structure and ecosystem functions, here decomposition. Such mismatches may result from the variable levels and paths of recovery communities are on in these frequently disturbed environments, preventing communities from reaching equilibrium and thus use available resources optimally (Fukami et al. 2010, Brose and Hillebrand 2016, Datry et al. 2016). Conversely, in hydrologically more stable, perennial sites, communities are more likely to be at equilibrium with their environment and their composition may better reflect resource availability and uses. As commonly found in the literature, microbially driven decomposition was little affected by flow intermittence, likely as a result of the microorganisms' capacities to (1) sustain activity during dry phases, especially if moisture is preserved and (2) to recover their activity within days to weeks of flow resumption (Foulquier et al. 2015, Arroita et al. 2018, Truchy et al. 2020).

River dendritic structure, i.e. multiple small streams branching into larger rivers, promotes gradual increases in biodiversity (Finn et al. 2011, Altermatt 2013) and metabolic activity (Diamond et al. 2021) as influx of organisms and resources (e.g. nutrients and dissolved organic matter) increase with water discharge from up to downstream. Because of this structure, communities in headwaters typically respond more strongly to disturbance than in the mainstem where mass dispersal can override the negative effect of disturbance (Tornwall et al. 2017). However, responses to natural drying can contrast with this pattern due to the fragmenting effect of drying, reducing connectivity and dispersal even in the mainstem (Crabot et al. 2020, Gauthier et al. 2020). We found that invertebrate richness responded more strongly to drying in the mainstem than in headwaters. This bigger loss of species with increasing intermittence in the mainstem sites may thus result from reduced mass effects in this fragmented network and from the higher richness typical of low-order perennial rivers, where communities have more to lose when facing a disturbance than already species-poor headwaters. We also found that invertebrate-driven decomposition increased with the distance to the source and was related to shredder abundance in headwaters only, agreeing with the theory that ecosystem functioning and BEF relationships should peak at intermediate levels of network connectivity (Leibold et al. 2017). Stronger relationship between decomposition and community multidimensional variability in headwaters than in mainstems may also reflect the high dependence of smaller, shaded streams on leaf resources and the stronger community specialization towards the use of leaf resource in the former. Contrastingly, microorganism-driven decomposition and leaf litter quality increased linearly with distance to the source, suggesting that microorganisms activity may increase from upstream to downstream, at least during the summer season, when microbial activity is likely boosted by higher temperature (Friberg et al. 2009). This may in turn increase leaf litter quality through microbial nitrogen immobilization from the water column.

The effects of drying on communities and ecosystem functions are relatively well documented at local reach scales (Datry et al. 2011, Foulquier et al. 2015), whereas network-scale responses owing to fragmentation remain overlooked, although evidence is emerging for fish (Jaeger et al. 2014) and invertebrate communities (Gauthier et al. 2020, Sarremejane et al. 2021). The proportion of perennial reaches upstream had a positive effect on leaf stocks, shredder abundance and invertebrate-driven decomposition, suggesting that connectivity to upstream perennial habitats is key in determining downstream leaf transfer (Catalàn et al. 2022), communities (Pineda-morante et al. 2022, Fournier et al. 2023) and ecosystem functions (Harvey et al. 2017). Interestingly, decomposition was higher when upstream connectivity was intermediate, suggesting that intermediate extents of flow intermittence upstream may promote higher functional rate in downstream habitats. In rivers, where the flux of resources and organisms is directional (i.e. dictated by the unidirectional flow of water), downstream ecosystem functions may thus depend on the disturbance regime in – and connectivity to – upstream habitats. An intermediate amount of upstream intermittence could therefore promote downstream decomposition rates by providing 1) pulses of high quality leaf resources and 2) influx of diverse species best adapted to resource use, from a variety of upstream habitats, following rewetting events (Northington and Webster 2017, del Campo et al. 2021a, Catalàn et al. 2022).

Decomposition is usually faster in aquatic than in riparian habitats due to moisture limitation hindering microbial activity and the presence of less efficient and abundant detritivore invertebrate communities in the latter (Hutchens and Wallace 2002, Tiegs et al. 2019, Lohse et al. 2020, Simões et al. 2021). Accordingly, we

found lower microorganism- and invertebrate-driven decomposition, shredder abundance and invertebrate richness in network-wide riparian habitats. We found weak evidence of relationships between instream and riparian invertebrate communities and changes along flow permanence gradients, suggesting that community overlap between these habitats was limited. Although long dry phases (i.e. > year) may lead to invertebrate community overlap between riparian and instream habitats due to convergences in environmental characteristics (Steward et al. 2022), the dry phases the Albarine experienced in 2021 were likely too short (< 2 months) to promote such community homogenization. However, the relationship between instream and riparian invertebrate-driven decomposition, and more weakly so instream and riparian invertebrate richness, changed with the distance to the source. The negative relationships observed in headwaters may suggest a compensation phenomenon where high invertebrate community richness and decomposing activity in riparian habitat may promote low richness and decomposition in adjacent instream habitats, and vice versa (Abelho and Descals 2019). This may occur if riparian decomposers use high quality compounds, leaving instream communities with lower quality resource entering through runoff, though we did not observe a negative relationship between leaf litter quality and quantity across both habitats. Conversely, microbial-led decomposition instream and in riparian habitats were positively related and this relationship was stronger among intermittent sites, suggesting that the microbial decomposer communities in both habitats may be related and more strongly so as flow intermittence increases. Instream and riparian microbial communities are likely to interact as suggested by compositional overlap between riparian soil and instream bacterial communities (Ruiz-González et al. 2015) and between senescent leaf and instream leaf-litter fungal communities (Koivusaari et al. 2019). Site-specific homogeneity in environmental characteristics such as humidity may also explain co-variability between riparian and instream microbial decomposition, particularly in headwaters where tree canopy may help preserving humidity in both the riparian and instream area.

Conclusion

Our results highlight the importance of flow intermittence on river meta-ecosystem dynamics and particularly on network-scale coarse organic matter cycling. Drying, by promoting the accumulation of unprocessed leaf litter, can affect the river network carbon processing and budget, modifying the timing and quantity of organic matter transport to recipient ecosystems (e.g. lakes, flood plains and oceans; Datry et al. 2018, Catalàn et al. 2022). However, intermediate drying extent could potentially stimulate ecosystem functions of downstream ecosystems. Our results are also some of the first to unravel the links between aquatic and terrestrial functioning in river networks from a large-scale field study (Scherer-lorenzen et al. 2022). By identifying where, when and under which conditions organic matter may accumulate and hotspots of decomposition occur, our research will help better predict impacts of climate change on biogeochemical cycles. As climate change exacerbate river drying in space and time, accounting for flow intermittence and its effects on both biodiversity and ecosystem functioning is also key to inform management actions that support healthy, functional ecosystems which deliver benefits to our societies, such as pollution attenuation (via microbial nutrient processing) and climate regulation (via carbon cycling; Palmer and Ruhi 2019).

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	Instream response variables	Hypothesis tested					
	Resource	Resource	Community structure	Community structure	Functioning	Functioning	
Predictor	Leaf stock	C/N	Taxa richness	Shredder abundance	Coarse-mesh bag K	Fine-mesh bag K	
Campaign	x	x	x	x	x	x	
Flow permanence (FP)	x	x	x	x	x	x	H1
Distance to the source (DS)	x	x	x	x	x	x	H2
Upstream connectivity (UC%)	x	x	x	x	x	x	H1, H2
Riparian response (RR)	x	x	x	x	x	x	H3,H4
Tree diversity	x	x					
Tree canopy cover	x						
Instream leaf stock			x	x	x	x	
Instream C/N			x	x	x	x	
Richness/Shredder abundance (R/A)					x		H5

	Instream response variables	Hypothesis tested					
	Interactions	Interactions	Interactions	Interactions	Interactions	Interactions	
Campaign * DS	x	x	x	x	x	x	H2
Campaign * FP	x	x	x	x	x	x	H1
Campaign * UC%	x	x	x	x	x	x	H1, H2
Campaign * RR	x	x	x	x	x	x	H3, H4
FP * DS	x	x	x	x	x	x	H1, H2
FP * UC%	x	x	x	x	x	x	H1, H2
RR * FP	x	x	x	x	x	x	H3
RR * DS	x	x	x	x	x	x	H4
UC * DS	x	x	x	x	x	x	H3, H4
R/A * UC%					x		H5
R/A * FP					x		H5
R/A * DS					x		H5

Table 1 : Set of predictors used in each global model, subjected to model selection and averaging. Richness and shredder abundance were each used as predictors for coarse-mesh bag decomposition rates (K) in separate models.

	Leaf stock	Leaf stock	C/N	C/N	T
	Transformation	log	log		
	Outlier removed	2	2	3	3
	No. models averaged	7	7	2	5
	Average adj. R ²	0.823	0.823	0.788	0
	Contrast	Est.	P	Est.	E
Season	Spring - Summer	-0.064	0.633	-26.645	<0.001
	Spring - Autumn	1.544	<0.001	-25.465	<0.001
Flow permanence (FP)		-0.244	0.027	8.071	0.002
Distance to source (DS)		0.069	0.342*	-14.332	<0.001
Upstream connectivity (UC%)		0.224	0.030		
Riparian response (RR)		0.100	0.105*		0
Tree diversity		0.093	0.159*		
Instream C/N					-0
Interactions	Interactions	Interactions	Interactions	Interactions	Interactions
Season * DS	Spring - Summer			<i>6.487</i>	<i>0.059</i>
	Spring - Autumn			11.028	0.001
Season * FP	Spring - Summer	0.059	0.655	-7.978	0.005
	Spring - Autumn	-0.346	0.014	<i>-5.173</i>	<i>0.064</i>
Season * UC%	Spring - Summer	-0.059	0.668*		
	Spring - Autumn	-0.374	0.005*		
FP * DS				<i>3.594</i>	<i>0.074*</i>
FP * UC%					0

	Leaf stock	Leaf stock	C/N	C/N	T
RR * FP					0
RR * DS					0

Table 2 : Results from LMM selection and averaging for resource and community variables. Adjusted R^2 (adj. R^2), P values (P) and estimates (Est.) were averaged among the models with a delta AICc < 2 from the best model. The number of averaged models, the transformation used on response variable, the number of outliers removed are also indicated. Bold and italic values indicate $P < 0.05$ and $P < 0.10$, respectively. * indicate variables that were selected in < 50% of the averaged best model, which we considered as secondary and less important.

Table 3 : Results from LMM selection and averaging for ecosystem functions, i.e. coarse- (CK) and fine- (FK) mesh bag decomposition. Adjusted R^2 (adj. R^2), P values (P) and estimates (Est.) were averaged among the models with a delta AICc < 2 from the best model. The number of averaged models, the transformation used on response variable, the number of outliers removed are also indicated. Bold values indicate $P < 0.05$. * indicate variables that were selected in < 50% of the averaged best model, which we considered as secondary and less important.

	CK	CK	FK	FK
	Transformation			
	3	3	2	2
	2	2	6	6
	0.652	0.652	0.737	0.737
	Est. $\times 10^{-3}$	P	Est. $\times 10^{-4}$	P
Season			5.502	<0.001
			0.693	0.672
Flow permanence (FP)	0.793	0.275*	-0.490	0.526
Distance to source (DS)	0.859	0.389	-0.359	0.672
Upstream connectivity (UC%)	4.409	0.039	1.496	0.308
Riparian response (RR)	-0.149	0.625	3.246	<0.001
Instream leaf stock			-1.024	0.047
Shredder abundance (Sab)	1.098	0.007		
Season * DS			8.223	<0.001
			0.965	0.367
Season * FP			0.960	0.241*
			2.456	0.009*
Season * RR			2.101	0.255
			-2.531	0.011
RR * FP			-1.413	0.008
RR * DS	1.087	0.002		
UC% * DS	5.430	0.015	2.543	0.103*
Sab * FP				
Sab * DS	-1.383	0.004		
Sab * UC%	-1.726	0.004		

	Quality	Quality	Community	Community	Functioning	Functioning
	F	P	F	P	F	P
Network location	18.108	0.001	3.092	0.002	2.427	0.088

	Quality	Quality	Community	Community	Functioning	Functioning
Habitat	19.661	0.001	27.624	0.001	71.860	0.001
Flow regime	1.034	0.326	3.173	0.001	7.314	0.002
Habitat * Network location	1.209	0.249	2.818	0.003	2.7403	0.103
Habitat * Flow regime	0.302	0.738	2.691	0.003	10.149	0.003
Network location * Flow regime	4.17	0.005	1.01	0.324	0.039	0.958

Table 4: Results from permutational analyses of variance (PERMANOVA)

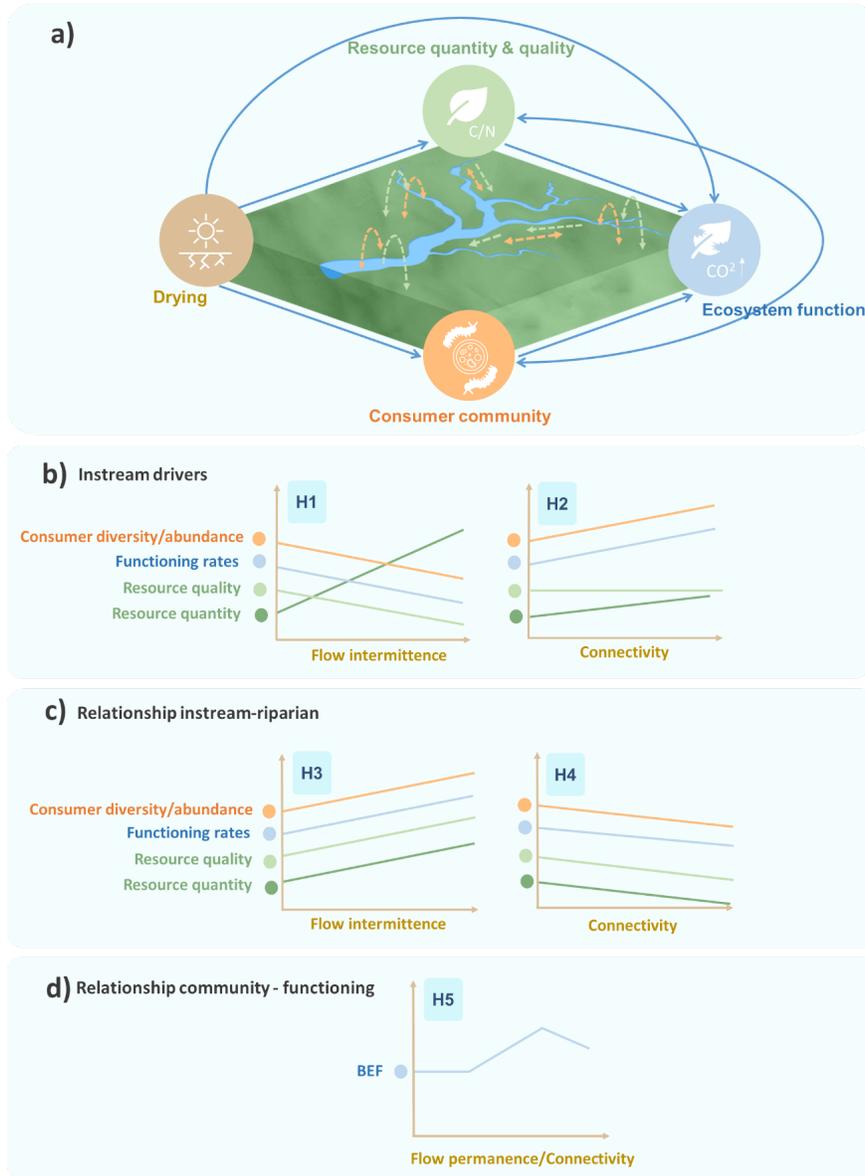


Fig. 1: Conceptual figure illustrating the links between resources, communities and functioning at the network scale (a); and the effects of increasing flow intermittence (drying) and network connectivity on instream

resource quantity and quality, consumer community diversity or abundance and functioning rates (b). Intermittence and connectivity may also affect the correlation between instream and riparian resource, community and functioning characteristics (c) and the correlation between consumers and ecosystem functioning (i.e. the biodiversity – ecosystem functioning [BEF] relationship, d)

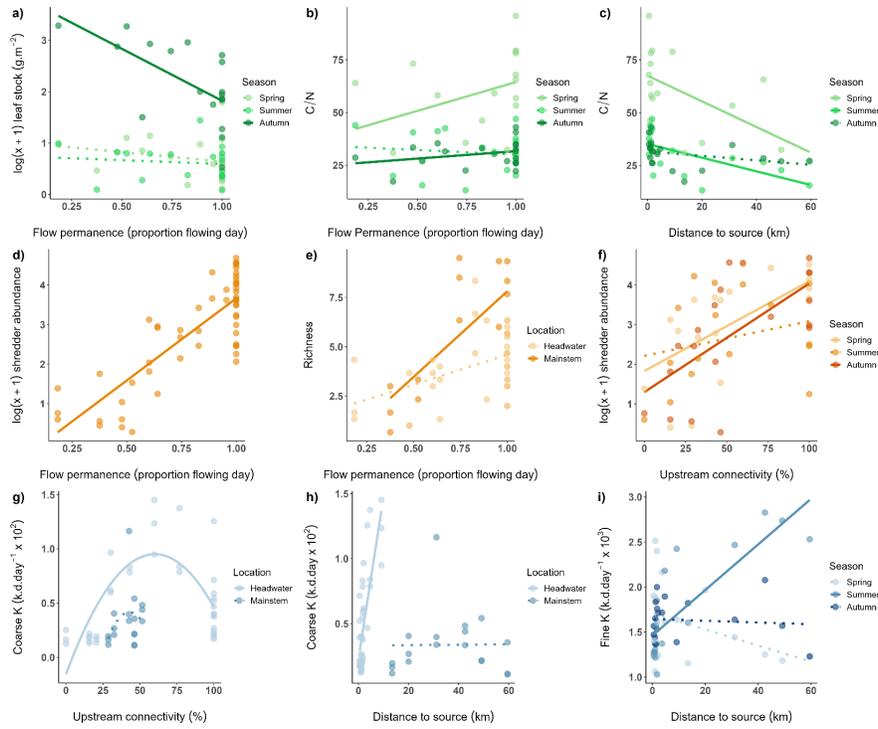


Fig. 2 : Responses of leaf resource characteristics (a-c), invertebrate community structure (d-f) and ecosystem functions (g-i) to flow permanence (FP), upstream proportion of perennial reaches (upstream connectivity: UC%) and upstream distance to the source (DS). Response variables include: leaf stock mass (a), carbon to nitrogen leaf contents (C/N; b-c), shredder abundances (d,f), invertebrate richness (e) and coarse and fine mesh leaf bag decomposition rates (Coarse K and Fine K, g-i). Full and dotted lines indicate significant and non-significant relationships, respectively. Responses were grouped by seasons, flow regime and locations to illustrate interactions. Regressions in (g) were fitted with a quadratic polynomial function.

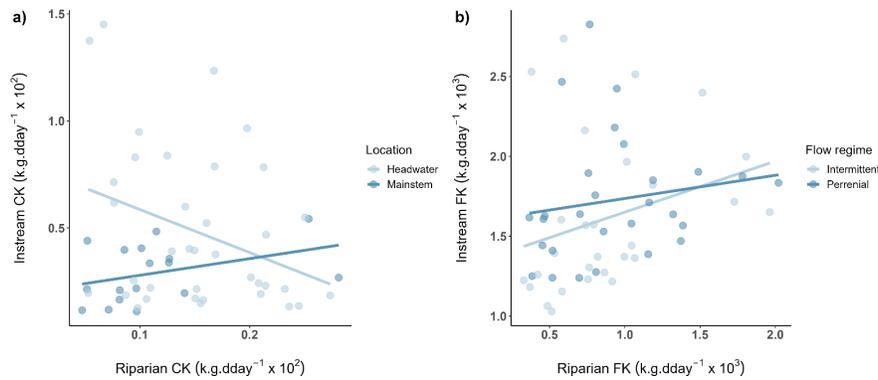


Fig. 3 : Relationships between instream and riparian decomposition driven by invertebrates (CK; a) and

microorganisms (FK; b) across network locations and sites with different flow regimes.

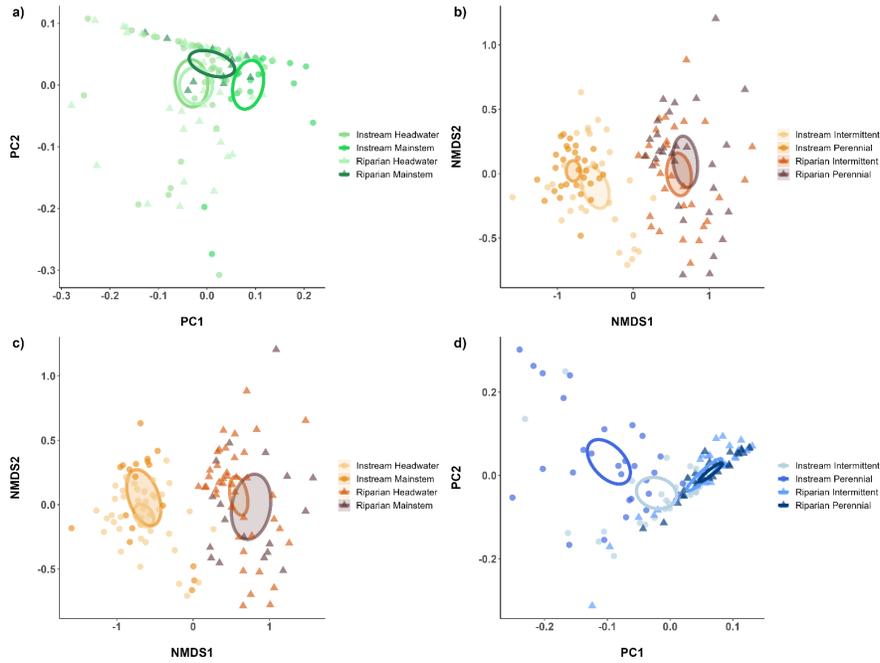


Fig. 4: Bidimensional ordinations showing variability in leaf characteristics (a), invertebrate communities (b,c) and decomposition rates (d) between instream and riparian habitats at sites with different flow regimes (intermittent vs. perennial) and network locations (intermittent and perennial). Only combinations showing significant (PERMANOVA; see Table 4) differences in leaf characteristics, community composition or decomposition between habitats are shown in this figure. Principal component analyses (PCA; a, d) and non-metric multidimensional scaling (NMDS; b, c) were used depending on data characteristics (see Material and Methods section).

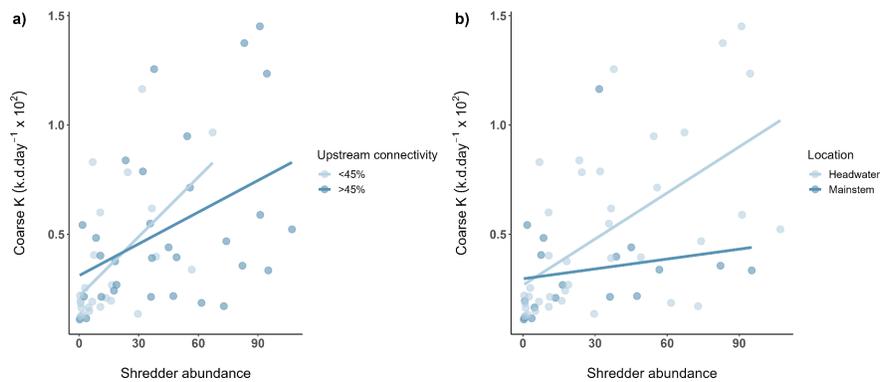


Fig. 5: Relationships between leaf-shredder abundance and invertebrate-driven decomposition (Coarse K) among sites with different levels of upstream connectivity (a) and network locations (b; headwater vs. mainstem)