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# **Ecohydrology of a macroinvertebrate metacommunity in a regulated floodplain**

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# Abstract

Floodplain ecosystems are some of the most biodiverse ecosystems on earth. This level of biodiversity is sustained by a great diversity of habitats and ecological niches, resulting from the interaction between the natural flow and sediment regimes. However, the ecological integrity of floodplains is rapidly deteriorating worldwide because of human activities. Flow regulation for hydropower production is one of the main drivers of ecological degradation in freshwaters and in floodplains in particular. Dams, impoundments and diversions result in a simplification of the natural flow regime, which becomes less variable, this in turn drives a simplification of the riverscape and a decrease in its biodiversity and ecological functioning. The general aim of this thesis is to investigate how communities of aquatic macroinvertebrates are shaped by hydrology in an alluvial floodplain in order to refine our understanding of hydrology – biodiversity linkages in complex ecosystems. To achieve this aim, I conducted an extensive field survey and an innovative field experiment on the Maggia River floodplain, in southern Switzerland. First, I investigated how different flooding regimes and recent flooding history lead to different community structures amongst floodplain habitats. I found that frequent flooding favored rheophilic species over more lentic groups, and limited strong competitive interactions to occur by maintaining low periphyton standing crops. Then, I developed a novel experimental setup, where 24 ponds were excavated out of two gravel bars in the floodplain, and monitored macroinvertebrate metacommunity assembly over 45 days. I showed that the interaction between the local environment and the degree of connectivity to the regional species pool can lead to different assembly trajectories through time. The findings of the experiment were then broadly compared to the temporal changes in metacommunity organization observed in the natural habitats. There, I found that local environmental conditions and the degree of landscape connectivity greatly affected metacommunity structure. Most importantly, I showed that metacommunity organization changed in time during post-disturbance metacommunity assembly, and that the temporal shifts between the main structuring processes differed with the dispersal ability of species. Finally, I used stable isotope analyses to calculate the food chain length within macroinvertebrate communities, and assessed how it responded to gradients of habitat size, productivity and disturbance regime. There, I showed that flooding reduced food chain length, because predators were feeding at lower trophic levels in frequently disturbed habitats. Overall, this study shows that maintaining flow variability and spatial heterogeneity in flood disturbance is key to sustaining floodplain aquatic biodiversity. My research also contributes to the field of metacommunity ecology by showing that metacommunity organization is highly variable in time and especially during assembly after disturbance.

# Résumé

Les zones alluviales sont l'un des biotopes à plus haute biodiversité sur notre planète. Cette biodiversité est due à la grande diversité d'habitats et de niches écologiques, résultant de l'interaction entre les régimes hydrologiques et sédimentaires naturels. Cependant, le statut écologique des zones alluviales connaît une rapide détérioration. La régulation des débits pour la production d'hydro-électricité est l'une des principales causes de la dégradation écologique des écosystèmes d'eaux douces et des zones alluviales en particulier. Les barrages et les dérivations entraînent une simplification du régime hydrologique, dont la variabilité est réduite, ce qui se traduit par une perte de biodiversité et de fonctionnement écologique. L'objet de ce travail est d'étudier l'effet du régime hydrologique sur les communautés d'invertébrés aquatiques d'une zone alluviale, dans le but d'améliorer notre compréhension des relations entre hydrologie et biodiversité dans les écosystèmes complexes. Mes recherches sont basées sur une campagne d'échantillonnage de terrain et une expérience novatrice effectuées dans la zone alluviale de la rivière Maggia, en Suisse. Dans un premier temps, j'ai étudié les processus directs et indirects liant le régime de crues et la structure des communautés d'invertébrés dans divers habitats de la zone alluviale. Cela a permis de montrer qu'une fréquence de crue élevée favorise les espèces rhéophiles, et limite le développement de fortes interactions compétitives entre espèces, en limitant la production primaire. Ensuite, j'ai utilisé une analyse d'isotope stables pour calculer la longueur de la chaîne alimentaire au sein des communautés d'invertébrés, et testé si elle variait avec différents niveaux de taille d'habitat, de productivité et de perturbation. J'ai montré que les chaînes alimentaires étaient plus courtes dans les habitats les plus souvent perturbés, car les prédateurs se nourrissaient à des niveaux trophiques plus bas. J'ai ensuite développé un système expérimental novateur, où nous avons creusé 24 étangs dans deux barres en gravier de la zone alluviale et suivi l'assemblage de la métacommunauté d'invertébrés durant 45 jours. J'ai montré que l'interaction entre les conditions environnementales locales et le degré de connectivité au réservoir d'espèces régional peut conduire à différentes trajectoires d'assemblage. Finalement, j'ai comparé les résultats de cette expérience avec les changements temporels d'organisation de la métacommunauté observés dans la zone alluviale. Cela a permis de montrer que les conditions environnementales locales mais aussi le degré de connectivité du paysage ont un très fort impact sur la structure de la métacommunauté. Mais surtout, j'ai montré que la structure de la métacommunauté change au cours de l'assemblage qui succède à une perturbation, et que la séquence temporelle dans les processus d'organisation de la métacommunauté diffère avec la capacité de dispersion des espèces considérées. Dans l'ensemble, ce travail montre que conserver la variabilité du régime hydrologique ainsi que l'hétérogénéité spatiale des perturbations (crues) est indispensable pour conserver la biodiversité aquatique dans les zones alluviales. Ma recherche contribue aussi à notre compréhension des métacommunautés, en montrant que l'organisation de la métacommunauté est très variable dans le temps, et surtout au cours de l'assemblage à la suite d'une perturbation.

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# Introduction

## General Background

Floodplains, the low-lying regularly flooded areas alongside river channels, are some of the most diverse ecosystems on earth (Tockner and Stanford 2002). Yet, human interventions are rapidly degrading their ecological integrity. In Europe for instance, 90% of floodplains are functionally extinct (Tockner and Stanford 2002) and 70% of floodplains have been destroyed in Switzerland alone since 1850 (Office Fédéral de l'Environnement, Suisse). The conflicts arising where human activities overlap with these natural zones of river expansion are often solved by constructing levees and embankments. These constructions disconnect the natural floodplain from the river channel and greatly impair its ecological and biogeochemical functioning. By reducing flow variability, river flow regulations and diversions also affect these ecosystems negatively because the ecological functioning of floodplains is so tightly dependent on the natural variability in discharge. Therefore, the rapidly rising global demand for hydropower puts a huge amount of pressure on floodplains and aquatic ecosystems in general. In order to ensure that the ecological integrity of floodplains can be maintained or restored, a sound understanding of the complex linkages between hydrology and biodiversity is needed.

## Floodplains: the dynamic habitat mosaic sustains high biodiversity

Floodplains are often described as dynamic habitat mosaics because they comprise an array of different aquatic and terrestrial habitats of which the spatial layout is regularly remodelled by floods (Stanford et al. 2005). The variety in aquatic habitat conditions results from differences in disturbance regimes and degrees of hydrological connectivity to the main channel and to groundwater (Amoros and Bornette 2002). Because of that great heterogeneity in habitat types and ecological niches in the floodplain, parafluvial aquatic habitats, the permanent or temporary aquatic habitats within the regularly flooded area, contribute disproportionately to biodiversity. Floodplains are pulsed ecosystems, where floods of different magnitude drive geomorphological, biogeochemical and ecological processes (Junk et al. 1989, Tockner et al. 1999, Stone et al. 2017). Large floods (exceedance probability <5%) remodel the geomorphological structure of floodplains and maintain a high habitat diversity, including side arms, ponds, backwaters, gravel bars and vegetated islands (Arscott et al. 2002; Van der Nat et al. 2003). Maintaining these large floods is therefore critical to maintaining geomorphological complexity, the template for habitat diversity. The more frequent, lower-magnitude floods play a major role in sustaining habitat heterogeneity and biodiversity at the floodplain scale by acting as spatially heterogeneous disturbances and by differentially connecting habitats. Physico-chemical attributes of parafluvial habitats are homogenized during phases of hydrological connection due to mixing and then diverge during disconnection phases, partly as a result of differing water sources (groundwater, side-tributaries, etc. Thomaz et al. 2007). These floods can affect biota either directly by removing or redistributing individuals (Matthaei et al. 1997, Bond and Downes 2000), thus resetting communities to earlier successional stages or by increasing ecological connectivity and therefore aquatic dispersal during inundation (Paillex et al. 2007, Gallardo et al. 2008, Fernandes et al. 2014). They also can indirectly affect biota by changing local habitat conditions and primary production (Paillex et al. 2013, Fernandes 2014,



Gallardo 2014). Because of the covariation between flood magnitude, environmental heterogeneity and lateral connectivity, beta diversity may either increase or decrease immediately after flooding. For instance, a relatively large flood could reduce beta diversity by filtering species according to their ability to resist high flows across habitats. Similarly, a flood may increase beta diversity either through spatially heterogeneous disturbance or through stochastic resampling of communities. In general, understanding how disturbance affects communities through deterministic or stochastic processes remains a central theme in ecology (Myers et al. 2015). In floodplains, HC is generally the main environmental gradient affecting communities, and is often pulsed during flood events. Generally, taxonomic richness in Ephemeroptera, Plecoptera and Trichoptera (EPT) is higher in well-connected habitats because these species need well-oxygenated and cold water (Usseglio-Polatera and Tachet, 1994). Contrastingly, richness in Coleoptera and Heteroptera peaks in isolated, stable environments (Arscott et al. 2005, Bonada et al. 2006, Skern et al. 2010, Gallardo et al. 2014). Taxonomic richness usually increases with HC, and peaks at intermediate levels (Ward 1998, Tockner et al. 1999, Gallardo et al. 2014, Whiles and Golowitz 2005). This likely supports the intermediate disturbance hypothesis (Connell 1978), where taxonomic richness is low in highly disturbed environments where only resistant species can survive, and also in very stable habitats where strong competitors outcompete other taxa. On the contrary, functional diversity tends to increase with hydrological isolation, and can also peak at intermediate levels, probably depending on the duration of the hydrological fragmentation period and environmental harshness. Functional diversity is low in highly connected environments because the frequent connectivity events may select only a small set of traits enabling species to survive in frequently disturbed environments (Paillex et al. 2013). In isolated habitats, functional diversity could either peak because strong competitive interactions force functional diversification (Hardin 1960, Paillex et al. 2013), or be low if environmental conditions are too harsh and therefore also select very specific traits (Gallardo et al. 2014). In spatially complex ecosystems like floodplains, the ecological connectivity between habitats also greatly affects the structure and functioning of communities, by influencing dispersal and colonization rates (Fernandes et al. 2014, Tonkin et al. 2016).

## **Metacommunities in dynamic landscapes**

Research is increasingly showing that ecological connectivity and dispersal play a central role in structuring communities. Thus, considering the ensemble of local communities as interacting parts of a metacommunity may notably contribute to our understanding of the processes maintaining biodiversity in complex dynamic landscapes. Metacommunities are traditionally defined as an ensemble of local communities linked by the dispersal of multiple, potentially interacting species, where both local interactions and regional processes influence community assembly (Leibold et al. 2004). By bridging local processes and spatial patterns, metacommunity ecology consists in understanding how local communities are structured and how they interact within a landscape. Four main metacommunity paradigms were originally described (Neutral theory, Patch Dynamics, Mass Effects and Species Sorting, see Leibold et al. 2004), yet it is now well accepted that metacommunities should rather be described along a continuum between Species Sorting (SS) and Mass Effects (ME) (Cottenie 2005), of which the position may be influenced by the strength of environmental filtering and dispersal rates (Lindström and Lagenheder 2012, Winegardner et al. 2012). Spatial control may be especially important, depending on the dispersal ability of species in relation to spatial distances and

connectivity levels (Heino et al. 2015, Datry et al. 2016, Thompson and Townsend 2006, Canedo et al. 2015).

In highly disturbed freshwater ecosystems, such as alluvial floodplains and intermittent rivers, the factors influencing the metacommunity structure (local environmental conditions and connectivity levels) may greatly vary in time, and this can result in temporal shifts in the processes structuring metacommunities (Fernandes et al. 2014, Datry et al. 2016, Sarremejane et al. 2017). In streams and floodplains, spatial control on communities tends to increase during high flows, reflecting local homogenization (Sarremejane et al. 2017, Chaparro et al. 2018), although other studies in floodplains have shown that environmental control increases during long inundation periods, suggesting that SS dominates when aquatic species are released from dispersal limitation and can track environmental variation (Dias et al. 2016, Fernandes et al. 2014).

### **Beyond structural attributes: the floodplain food web**

The effects of hydrology and associated environmental gradients on structural aspects of local communities have been extensively studied, but responses at the functional level remain poorly understood. Because trophic interactions can play a particularly important role in structuring ecological communities in floodplains, especially during phases of hydrological disconnection (Townsend et al. 1997, Fairchild et al. 2000, Mouquet et al. 2003, Cadotte 2007), understanding how food web attributes such as food chain length vary in response to environmental conditions and hydrology could greatly improve our understanding of floodplain ecosystems. Food webs describe the feeding links between species within communities, and the food chain length is a key attribute of food webs, known to influence species diversity, community structure and stability (reviewed in Sabo et al. 2009). Recent research shows that better knowledge of food web response to environmental drivers can improve our understanding of environment-biota relationships in heterogeneous landscapes such as alluvial floodplains (Thompson et al. 2012, Bellmore et al. 2013).

**Aim of the study:** The overarching aims of this thesis were, first, to examine the complex effects of floodplain hydrology on structural and functional aspects of macroinvertebrate communities, and second, to assess specifically how landscape connectivity, disturbance and temporal changes in environmental conditions affected metacommunity organization through time.

**In chapter 1,** I investigated the relative effects of flood frequency, magnitude and time elapsed since the last flood on macroinvertebrate communities of 24 parafluvial habitats in the Maggia river floodplain, Switzerland. Parafluvial habitats were sampled seasonally over one year and a combination of 2D hydrodynamic modelling and piecewise structural equation modelling was used to quantify the direct and indirect effects of local hydrological metrics on macroinvertebrate communities.

**In chapter 2,** I created 24 ponds in two gravel bars within the floodplain, differing in levels of hydrological and landscape connectivity (i.e. distance to source habitats of potential colonists). I measured ecosystem properties and aquatic macroinvertebrates over 45 days to assess the relative strength of processes contributing to community composition and functional diversity.

**In chapter 3**, I characterized invertebrate communities and local habitat conditions before and at regular intervals after a major flood. First, I examined patterns of diversity in environmental conditions and macroinvertebrate communities over time. Then, I explored the temporal variation in structuring processes affecting the metacommunity of aquatic macroinvertebrates and asked whether it would change with the dispersal ability of species.

**In chapter 4**, I investigated how food chain length, a central aspect of food webs, varied among floodplain habitats and asked whether habitat size, productivity and disturbance regime could explain this variation.

As a whole, this work aims at providing insights into the complex effects of hydrology on the structure and functioning of a macroinvertebrate metacommunity in a regulated floodplain. The final section of this thesis summarizes the main findings and discusses their implications for the management of river floodplains and for ecological research in general.

## References

- Amoros, C., and Bornette, G. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology* 47: 761-776.
- Arscott, D. B., Tockner, K., Van der Nat, D., and Ward, J. V. 2002. Aquatic Habitat Dynamics along a Braided Alpine River Ecosystem (Tagliamento River, Northeast Italy). *Ecosystems* 5:802-814
- Arscott D.B., Tockner K. & Ward J.V. (2005) Lateral organization of aquatic invertebrates along the corridor of a braided floodplain river. *Journal of the North American Benthological Society*, 24, 934–954.
- Bellmore, J. R., Baxter, C. V., Martens, K. and Connolly, P. J. 2013. The floodplain food web mosaic: a study of its importance to salmon and steelhead with implications for their recovery. *Ecological Applications*, 23: 189-207. doi:10.1890/12-0806.
- Bonada N., Rieradevall M., Prat N. & Resh V.H. (2006) Benthic macroinvertebrate assemblages and macrohabitat connectivity in Mediterranean-climate streams of northern California. *Journal of the North American Benthological Society*, 25, 32–43.
- Bond N. R., and Downes B. J. 2000. Flow-related disturbance in streams: an experimental test of the role of rock movement in reducing macroinvertebrate population densities. *Marine and Freshwater Research* 51, 333-337.
- Cadotte, M. W. 2007. Competition-colonization trade-offs and disturbance effects at multiple scales. *Ecology* 88:823- 829.
- Canedo-Arguelles, M. et al. 2015. Dispersal strength determines meta-community structure in a dendritic riverine network. – *J. Biogeogr.* 42: 778–790.
- Chaparro G, Horváth Z, O'Farrell I, Ptacnik R, Hein T. 2018. Plankton metacommunities in floodplain Islands under contrasting hydrological conditions. *Freshwater Biol*, 63:380–391.
- Connell J. 1978. Diversity in tropical rainforests and coral reefs. *Science*, 199 ,1302–1310.
- Datry, T., Bonada, N., and Heino, J. 2016. Towards understanding the organization of metacommunities in highly dynamic ecological systems. *Oikos* 125: 149-159.
- Dias, J.D., Simões, N.R., Meerhoff, M., Lansac-Tôha, F. A., Machado Velho, L. F., and Bonecker, C. C. 2016. Hydrological dynamics drives zooplankton metacommunity structure in a Neotropical floodplain. *Hydrobiologia* 781: 109-125
- Fairchild, G. W., Faulds, A. M., and Matta, J. F. 2000. Beetle assemblages in ponds: effects of habitat and site age. *Freshwater Biology* 44: 523-534.
- Fernandes, I. M., Henriques-Silva, R., Penha, J., Zuanon, J., and Peres-Neto, P. R. 2014. Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities. *Ecography* 37: 464-475.
- Gallardo, B., Doledec, S., Paillex, A., Arscott, D. B., Sgeldon, F., Zilli, F., Mérigoux, S., Castella, E., and Comin, F. A. 2014. Response of benthic macroinvertebrates to gradients in hydrological connectivity: a comparison of temperate, subtropical, Mediterranean and semiarid river floodplains. *Freshwater Biology* 59: 630-648.
- Gallardo, B., Garcia, M., Cabezas, A., Gonzalez, E., Gonzalez, M., Ciancarelli, C., and Comin, F. A. 2008. Macroinvertebrate patterns along environmental gradients and hydrological connectivity within a regulated river-floodplain. *Aquatic Sciences* 70: 248-258.
- Hardin, G. (1960) Competitive exclusion principle. *Science*, 131, 1292–1297.

- Heino, J., Melo, A. S., Siquiera, T., Soininen, J., Valanko, S., and Bini, L. M. 2015. Metacommunity organisation, spatial extent, and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology* 60: 845-869
- Junk, W. J., P. B. Bayley and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. *Canadian Special Publications of Fisheries and Aquatic Sciences*. 106:110-127.
- Leibold, M., A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J., B., Law, R., Tilman, D., Loreau, M., and Gonzalez, A. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7: 601-613
- Lindström, E. S., and Lagenheder, S. 2012. Local and regional factors influencing bacterial community assembly. *Environmental Microbiology Reports*, 4:1-9.
- Matthaei, C. D., Irthmüller, D., Frutiger, A. 1997. Invertebrate recovery from a bed-moving spate: the role of drift versus movements inside or over the substratum. *Archiv für Hydrobiologie* 140:221-235.
- Mouquet, N., Munguia, P., Kneitel, J. M., and Miller, T. E. 2003. Community assembly time and the relationship between local and regional species richness. *Oikos*, 103: 618-626.
- Myers, J. A., Chase, J. M., Crandall, R. M. and Jiménez, I. 2015. Disturbance alters beta-diversity but not the relative importance of community assembly mechanisms. *J Ecol.* 103: 1291-1299.
- Office Fédéral de l'Environnement OFEV ([www.bafu.admin.ch](http://www.bafu.admin.ch))
- Paillex, A., Castella, E., and Carron, G. 2007. Aquatic macroinvertebrate response along a gradient of lateral connectivity in river floodplain channels. *Journal North American Benthological Society* 26: 779-796.
- Paillex, A., Doledec, S., Castelly, E., Mérigoux, S., and Aldridge, D. C. 2013. Functional diversity in a large river floodplain: anticipating the response of native and alien macroinvertebrates to the restoration of hydrological connectivity. *Journal of applied ecology* 50: 97-106.
- Sabo J.L., Finlay J.C., and Post D. M. 2009 Food chains in freshwaters. *The Year in Ecology and Conservation Biology, 2009: Ann NY Acad Sci* 1162: 187–220.
- Sarremejane R, Cañedo-Argüelles M, Prat N, Mykrä H, Muotka T, and Bonada N. 2017. Do metacommunities vary through time? Intermittent rivers as model systems. *Journal of Biogeography* 44: 2752–2763.
- Skern M., Zweimueller I. & Schiemer F. 2010. Aquatic Heteroptera as indicators for terrestrialisation of floodplain habitats. *Limnologica*, 40, 241–250.
- Stanford, J. A., M. S. Lorang and F. R. Hauer. 2005. The shifting habitat mosaic of river ecosystems. *Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen*. 29(1):123-136.
- Stone M.C., Byrne C.F., and Morrison R.R. 2017. Evaluating the impacts of hydrologic and geomorphic alterations on floodplain connectivity. *Ecohydrology* 10:e1833.
- Thomaz, S. M., Bini, L. M., and Bozelli, R. L. 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia* 579: 1-13
- Thompson, R. M. et al. 2012. Food webs: reconciling the structure and function of biodiversity. – *Trends. Ecol. Evol.* 27: 689-697.

- Thompson, R., and Townsend, C. 2006. A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. *Journal of Animal Ecology* 75: 476-484
- Tockner, K., Pennetzdorfer, D., Reiner, N., Schiemer, F. and Ward, J. V. 1999. Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river–floodplain system (Danube, Austria). *Freshwater Biology*, 41: 521-535
- Tockner, K. and Stanford, J. A. 2002. Riverine flood plains: present state and future trends. *Environmental Conservation* 29: 308–330.
- Tonkin, J., Stoll, S., Jähnig, S., and Hase, P. 2016. Contrasting metacommunity structure and beta diversity in an aquatic-floodplain system. *Oikos* 125: 686-697.
- Townsend C. R., Scarsbrook M. R, Dolédec S.1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams, *Limnology and Oceanography*, 42: 938-949
- Usseglio-Polatera P. & Tachet H. (1994) Theoretical habitat templates, species traits, and species richness – Plecoptera and Ephemeroptera in the Upper Rhône River and its floodplain. *Freshwater Biology*, 31, 357–375.
- Van Der Nat, D., Tockner, K, Edwards, P. J., Ward, J. and Gurnell, A. M. 2003. Habitat change in braided flood plains (Tagliamento, NE-Italy). *Freshwater Biology*, 48: 1799-1812
- Ward, J.V., 1998. Riverine landscapes: Biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation* 83: 269 – 278
- Whiles, M. R. and B. S. Goldowitz, 2005. Macroinvertebrate communities in Central Platte River wetlands: Patterns across a hydrologic gradient. *Wetlands* 25: 462 – 472
- Winegardner, A. K., Jones, B. K., Ng, Y. S. Y., Siqueira, T., and Cotneie, K. 2012. The terminology of metacommunity ecology. *Trends in Ecology and Evolution* 73:253-254.

# Chapter 1

# Direct and indirect effects of flood regime on macroinvertebrate assemblages in a floodplain riverscape

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**Running head:** Effect of flood regime on floodplain macroinvertebrate communities



**Abstract:** Floods are necessary for the functioning of floodplain ecosystems. Ultimately, flood effects on biota are spatially complex and unfold at various time scales. Yet, biodiversity conservation in regulated floodplains requires a sound quantification of the main pathways how floods affect riverine ecosystems. Here, we investigated the relative effects of flood frequency, magnitude and time elapsed since the last flood on macroinvertebrate communities of 24 parafluvial habitats in the Maggia river floodplain, Switzerland. Parafluvial habitats were sampled seasonally over one year and a combination of 2D hydrodynamic modelling and piecewise structural equation modelling was used to quantify the direct and indirect effects of local hydrological metrics on macroinvertebrate communities. We found that high flood frequency favoured rheophilic species (EPT taxa) over other groups (Coleoptera, Diptera) and prevented strong competitive interactions and competitive exclusion by maintaining low food resource levels. Importantly, we found that parafluvial habitats exhibited more lentic-like characteristics as time passed after a flood, which caused EPT taxa to be relatively more abundant and taxa richness higher immediately after flood disturbance. Lastly, overall taxa richness increased over time after a flood and even more so after larger floods. Our results suggest that variation in flood magnitude, frequency and return period maximizes beta diversity within floodplain riverscapes due to the independent and spatially-interactive responses of parafluvial habitats.

**Keywords:** floodplain, flood regime, stream invertebrates, ecological succession

## Introduction

Alluvial floodplains are widely recognized as valuable features of our landscapes, for the goods and services they provide humans and for their intrinsic ecological value and high biodiversity (Tockner et al. 2010). Despite these values, human activities still threaten their integrity and ecological status globally by directly altering their morphological structure and natural flow regimes. For instance, 90% of floodplains are functionally extinct in Europe (Tockner and Stanford 2002). Preserving or restoring spatial heterogeneity in flow regimes (flooding) is a much-recommended measure in floodplain restoration (Paillex et al. 2009, 2013), yet restoring the natural flow regime in regulated rivers is rarely an option and instead compromises must be made between hydropower production, flood protection and ecological values.

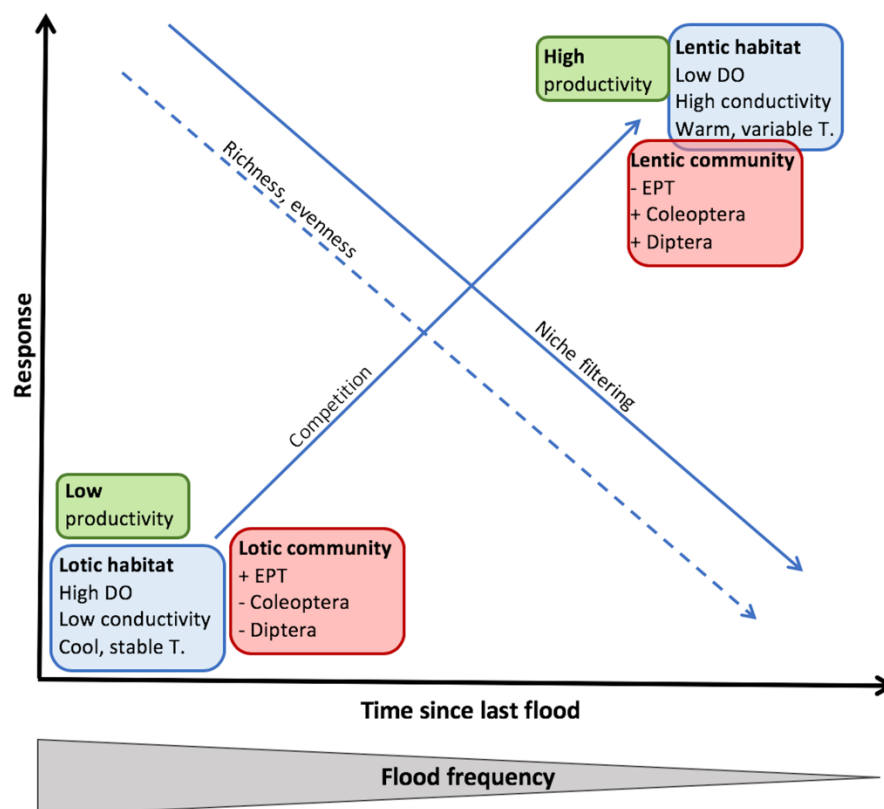
Indeed, floodplains are pulsed ecosystems, where floods of different magnitude drive geomorphological, biogeochemical and ecological processes (Junk et al. 1989, Tockner et al. 1999, Stone et al. 2017). In particular, large floods (exceedance probability <5%) remodel the geomorphological structure of floodplains and maintain a high habitat diversity, including side arms, ponds, backwaters, gravel bars and vegetated islands (Arscott et al. 2002; Van der Nat et al. 2003), thus sustaining high biodiversity (Stanford et al. 2005, Datry et al. 2014).

In addition, low-to-medium magnitude floods exert a strong influence on primary production and biota within floodplains. During the flood, so called connection phase, organic matter and nutrients are exported to the floodplain, which triggers an increase in primary production when the flood recedes, so called disconnection phase (Tockner et al. 1999, Tockner et al. 2000, Ahearn et al. 2006). Lesser magnitude floods also affect biota directly through the mechanical removal/redistribution of individuals (Matthaei et al. 1997, Matthaei et al. 1999, Bond and Downes 2000) or increased ecological connectivity and dispersal during inundation (Paillex et al. 2007, Gallardo et al. 2008, Fernandes et al. 2014). They also can indirectly affect biota by changing local habitat conditions and primary production (Paillex et al. 2013, Fernandes 2014, Gallardo 2014). For instance, flooding scours bottom substrata and displaces individuals, thereby resetting communities to earlier successional stages (Amoros and Bornette 2002, Thomaz et al. 2007). Because parafluvial habitats have different thresholds and frequencies of inundation, the floodplain is often described as a mosaic of habitats at different successional stages (Bravard et al. 1986, Salo et al. 1986, Mouw et al. 2013, Whited et al. 2007).

Local physico-chemical conditions among parafluvial habitats largely result from the interaction between habitat positions within the geomorphological settings of the floodplain, which, e.g., determines water sources such as groundwater inputs (Malard et al. 2007, Capderrey et al. 2014). Local conditions also vary with the level of lateral connectivity to the main channel and vertical connectivity with alluvial aquifers, both of which can be pulsed or constant over time (Amoros and Bornette 2002, Brunke et al. 2003, Opperman et al. 2010, Capderrey et al. 2014). More specifically, physico-chemical attributes of parafluvial habitats are homogenized during phases of hydrological connection due to mixing and then diverge during disconnection phases, partly a result of differing water sources (groundwater, side-tributaries, etc.) and different properties in ecological succession (Thomaz et al. 2007). For example, typical habitat responses to decreases in hydrological connectivity include increases in electrical conductivity and ammonium concentration (Paillex et al. 2007, Paillex et al. 2009, Larned and Datry 2013), and decreases in dissolved oxygen (Gorski et al. 2013, Scott et al. 2011, Larned and Datry 2013). Nutrient concentrations in parafluvial habitats also tend to increase with connectivity to the main channel and with groundwater seepage, but are also affected by water retention time as well as

biological processes (Amoros and Bornette 2002, Brunke et al. 2003, Larned and Datry 2013). Lastly, water temperature is affected by connectivity gradients as well, where habitats with groundwater inputs typically have more constant temperatures through the year (Amoros and Bornette 2002, Larned and Datry 2013). These differences in local abiotic conditions driven by hydrological connectivity constrain biotic assemblages within parafluvial habitats of the floodplain (Brunke et al. 2003, Starr et al. 2014, Cadotte et al. 2017).

The coupling of environment-biota relationships is ubiquitous in fluvial systems, but parafluvial floodplain habitats are particular in that environmental conditions evolve over time during disconnection phases, effectively creating a time-varying environmental filter on biotic communities (Chang et al. 2016, Cadotte et al. 2017). For instance, macroinvertebrate assemblages are constrained by the dispersal mode of organisms in relation to the distance to potential sources of colonists following a flood and, mass effects excluded, by local conditions, resource availability and inter-patch hydrological connectivity (Amoros and Bornette 2002, (Tonkin et al. 2016). In the initial phase of colonisation, strong aerial dispersers can colonize habitat patches in priority, tracking favourable environmental conditions (Leibold et al. 2004, Cadotte 2007, Soininen 2014) as local habitat conditions diverge; i.e., the local environment dictates assemblage composition (Chang et al. 2016). As time passes after a flood, competitive interactions can gain importance as a structuring force of communities, see Figure 1 (Fairchild et al. 2000, Mouquet et al. 2003, Cadotte 2007).



**Figure 1.** Conceptual diagram outlining the effects of flood frequency and time since last flood on community assembly rules (full arrows), taxa richness and evenness (dashed arrow), primary productivity, abiotic conditions and community composition.

Species functional traits in relation to dispersal ability and niche breadth can be particularly useful in identifying the relative importance of specific processes such as environmental filtering in structuring communities (Thompson and Townsend 2006, Smith et al. 2015, Tonkin et al. 2016). Functional diversity, commonly defined as “the value and range of the functional traits of the organisms in a given ecosystem” (Diaz and Cabido 2001, Tilman 2001), has often been used by community ecologists to infer community assembly rules. This approach is based on the assumption that communities structured by the environment have low functional diversity because only adapted phenotypes (corresponding to specific ecological niches) are selected by the environmental filter (van der Valk et al. 1981, Keddy 1992, Diaz et al. 1999). In contrast, communities structured by strong interspecific competitive interactions have high functional diversity as a result of limiting similarity processes such as niche partitioning, whereby only species occupying non-overlapping ecological niches can co-occur (MacArthur and Levins 1967, Cornwell et al. 2009). In cases where strong competition leads to competitive exclusion, functional diversity also is low (Kraft et al. 2015, Cadotte et al. 2017, Passy et al. 2017). Although patterns of functional diversity must be interpreted with caution, they still provide robust evidence for different community assembly mechanisms when associated with sound understanding of the study system (Paillex et al. 2013, Li et al. 2015, Cadotte et al. 2017, Passy et al. 2017).

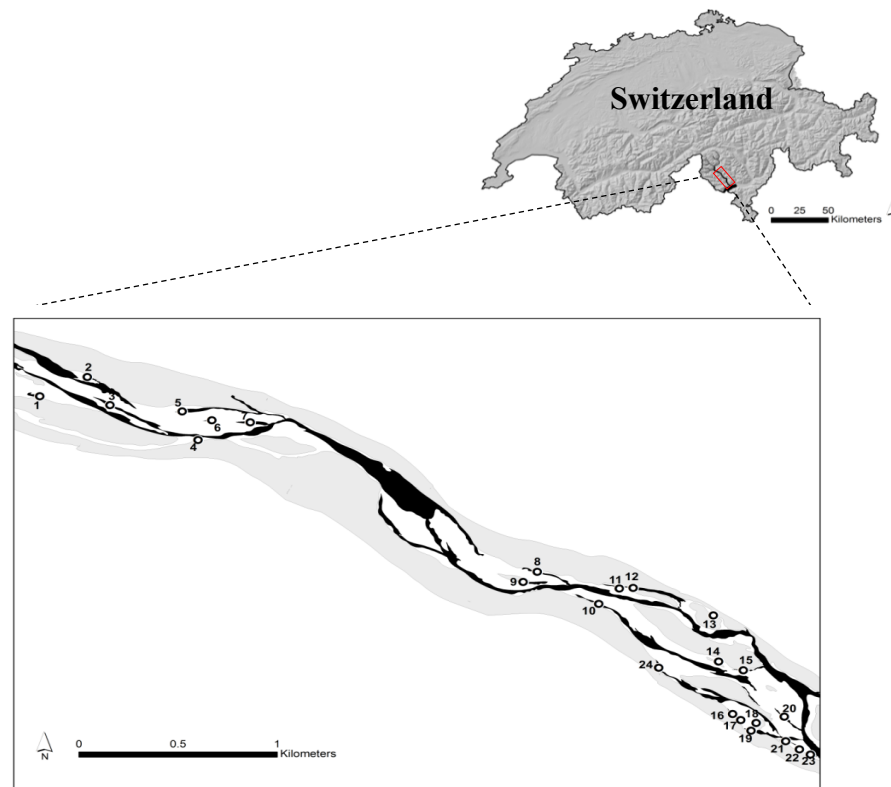
In this study, we aimed at quantifying the relative effects of long-term flood regime and recent flood history on macroinvertebrates inhabiting parafluvial habitats within a regulated floodplain riverscape. We sampled 24 parafluvial habitats seasonally for one year in a heterogeneous floodplain and developed a 2D hydrodynamic model of the floodplain to derive flooding frequencies and flood history. A piecewise structural equation modelling approach (SEM) was used to quantify the direct and indirect effects of flood regime through changes in local habitat and resource availability on the macroinvertebrate communities. We hypothesized that recent disturbance history (time elapsed since last flood) would be the main constraint of local habitat conditions and biota, with habitat characteristics ( $H_1$ ) and communities ( $H_2$ ) transitioning from lotic-like to lentic-like over time. Specifically, the time elapsed since last flood would affect the community composition directly by favouring strong dispersers early in assembly and indirectly through temporal changes in habitat conditions. Further, we anticipated that biofilm standing crops (food resource) would be lower in frequently flooded sites but increase over time after a flood ( $H_3$ ), and that decreased biofilm standing crop would lead to increased competitive interactions and decreased community evenness ( $H_4$ ).

## Methods

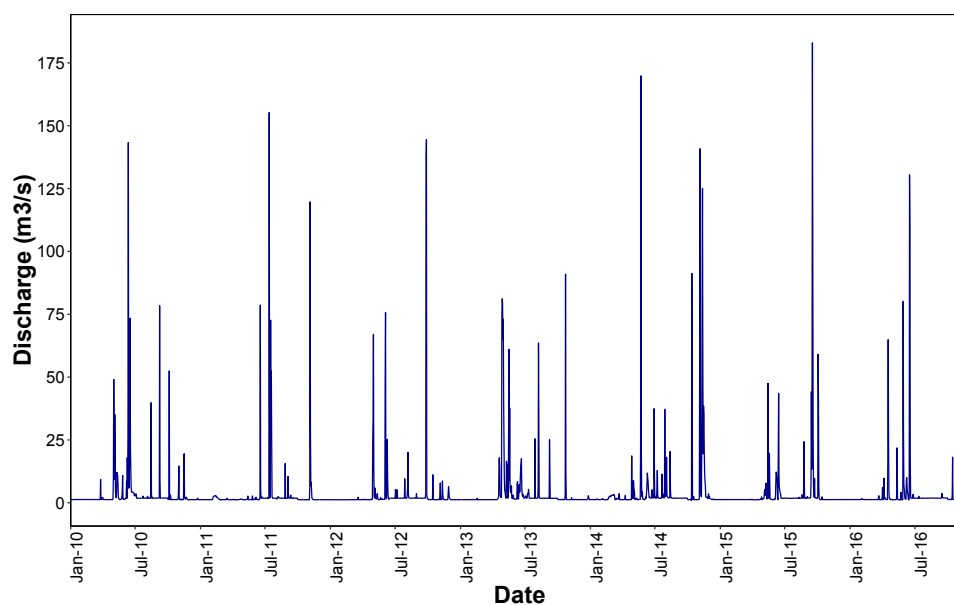
### *Study site*

The Maggia river is located in the south-eastern part of the Swiss Alps and flows southward into Lake Maggiore (Figure 2). It is one of the last remaining natural (non-urbanized) floodplains in Switzerland, and therefore has been declared a site of national importance (Kuhn and Amiet 1988). Its catchment covers an area of 930 km<sup>2</sup> with elevations ranging from 200 to 3300 m a.s.l. Owing to the presence of two glaciers in the headwaters and snowfall precipitation in winter, the hydrological regime is classified as glacionival. Following the construction of a complex hydropower scheme in the headwaters in 1953, the flow regime of the river has been substantially modified (Pfamatter and Zanetta 2003, Molnar et al. 2008). The original high flows during snowmelt have been replaced by essentially constant flows (minimum flow requirements

$\sim 1.5 \text{ m}^3/\text{s}$ ) with occasional flood peaks (Figure 3) with no correlation between magnitude and return period (Molnar et al. 2008, Perona et al. 2009). The alluvial floodplain used in this study is located in the middle of the valley; it is about 7-km long and nearly 2-km wide in some sections. Because of the fairly low storage of the hydropower scheme and high lateral hillslope runoff during major rain events, the larger flood peaks still occur (Figure 3) but the lesser magnitude floods do not (under  $\sim 10 \text{ m}^3/\text{s}$ ).



**Figure 2.** Map of Switzerland showing the location of the Maggia River floodplain and the parafluvial habitats sampled.



**Figure 3.** Hydrograph of the Maggia River upstream of the modelling domain (gauging station Bignasco), from January 2010 to November 2016.

The combination of high flows and an abundance of bedload sediment (mean diameter of stones = 120 mm) maintains a diverse floodplain habitat. Within the floodplain, single-thread sections alternate with braided reaches where various types of parafluvial habitats occur: ponds, connected and disconnected side arms, and backwaters. For this study, we selected 24 permanently-wetted parafluvial habitats, specifically permanent ponds, disconnected side arms, and side arms connected at their downstream end with a shallow riffle.

#### *Field sampling & laboratory analysis*

Samples were collected once per season: in February 2016, in May 2016, August 2016 and October 2016. On each visit, a water sample (0.5 L) was collected from each habitat and stored on ice in the dark for chemical analysis in the laboratory. In the laboratory, water samples were analyzed for calcium (Ca, mg/L), nitrate (NO<sub>3</sub>, mg/L), and pH using standard methods following Tockner et al. (1997). Spot measurements of dissolved oxygen (mg/L, Hach HQ40d connected to a LD10101 oxygen probe), water temperature (°C), and electrical conductivity (µS/cm, WTW meter, Germany) also were taken on each visit. At each sampling event, the order in which water samples and physico-chemical variables were measured was randomized among ponds to reduce bias of collection time. Additionally, a temperature sensor-logger (Thermocron, i-button) was deployed within each habitat for a period of 7 days following each visit that recorded water temperature hourly. The mean, standard deviation, range, minimum and maximum water temperatures were then calculated for each site and each season. Substrate size composition was measured using the zig-zag pebble count method where 50 cobbles were randomly selected along a reach and their b-axis measured (King et al. 1995). The structural diversity of the substratum within each habitat was calculated using the Shannon-Wiener index  $H$  (Cellot et al. 1994, Burnett et al. 1998, Brunke et al. 2003):

$$H = - \sum_{i=1}^S (p_i \ln(p_i))$$

With  $S$  being the number of Wentworth substrate size classes (Wentworth et al. 1922, Table S1 in supporting information) and  $p_i$  the proportion of the total sample belonging to the  $i$ th size class.

Surface biofilms (periphyton) were measured by randomly selecting 5 stones (cobble-size) within each habitat. The biofilm was removed from each stone by scrubbing with a wire brush into a plastic container with 100 mL of distilled water, and the scrubbed area measured (after Uehlinger 1991). The biofilm suspension was subsequently filtered through a glass fiber filter (0.45 µm, Whatman GFF) and stored on ice in the dark. Chlorophyll-a extraction was conducted by incubating each half-filter in 6 mL 90% ethanol at 70°C for 10 minutes. Chlorophyll-a (µg /L) was then determined using standard spectrophotometry (Hitachi 2000) following methods in Meyns et al. (1994). In parallel, the other half of each filter was dried at 60°C for 24h, weighed, then combusted at 450°C for 6h and reweighed for estimates of organic matter biomass as AFDM. Benthic macroinvertebrates were randomly collected ( $n = 3$ , at each site and date) using a Hess sampler (250 µm mesh, 0.04 m<sup>2</sup> area) and preserved in 70% ethanol. In the laboratory, collected individuals were hand-picked, counted and identified to the lowest

possible taxonomic level using Tachet et al. (2010). Of all taxa, 88% were identified to the family level, 6% to the class level and 6% to the order level.

### *Data analysis*

*Macroinvertebrate metrics* - Macroinvertebrate taxa richness and community evenness were calculated for each site. To assess changes in community composition we also used the relative proportion (%) of the major groups: Coleoptera, Ephemeroptera, Plecoptera, Trichoptera, and Diptera. Functional diversity (FD) was calculated as the standardized effect size of Rao's quadratic entropy (SES-RaoQ), calculated as the standard deviation of the observed RaoQ from that of a null model. The null model was constructed by shuffling species abundances within each site and calculating RaoQ at each of 999 iterations. This type of null model approach, commonly used in functional diversity studies, has the advantage of removing the influence of differences in species richness on FD (Mason et al. 2013). For the analysis, we used all biological traits available in our database and used in previous studies on floodplain systems (e.g., Paillex et al. 2013, Van der Vorste et al. 2016), amounting to 41 categories distributed in 9 biological traits (Table S2, Supporting Information). Functional traits for all taxa were obtained from the Tachet database for each taxon (Tachet et al. 2010). To give the same weight to all traits in the diversity measure, affinity scores were standardized so that their sum for a given taxon would equal 1 (see Paillex et al. 2013).

*Hydrodynamic model*- We developed a 2D hydrodynamic model for the floodplain which enabled us to calculate two key hydrological metrics for each habitat: flood frequency over the two years preceding a sampling event and recent disturbance history represented by the number of days elapsed since the last flood. The model was constructed using Basement software (Faeh et al. 2010, developed at ETH Zurich: <http://www.basement.ethz.ch/>), which solves the depth-averaged shallow-water Saint-Venant equations to calculate water depth, current velocity and bottom shear stress for each element within the modelling domain. Because of the spatial complexity of groundwater-surface water interactions in this alluvial floodplain that cannot be accurately simulated under the current state of system characterization, we only used the model to derive thresholds of discharge at which a given habitat becomes inundated with surface water as well as local bottom shear stress. Our modelling approach consisted of running steady-state simulations for the range of discharges corresponding to flood peaks that occurred between 13 March 2014 and the end of our study period on 28 October 2016. During this period, 45 identified flood events occurred (Table S3, Supporting Information), with a maximum discharge of 570 m<sup>3</sup>/s. For each discharge simulation, the model produced a simulated water depth for each cell of the modelling domain which was then overlapped with a map of our sampling sites to determine whether a particular habitat was flooded at a given discharge. We were then able to calculate a flood frequency for each habitat during the modelling period as well as the time elapsed since the last flood at each sampling campaign (February, May, August and October). We used the bottom shear stress values calculated by the model as a proxy for flood magnitude, as the effect of flooding on macroinvertebrates is dependent on bottom shear stress values (Borchardt 1993, Gibbins et al. 2007, Gibbins et al. 2009).

Floodplain bathymetry was obtained from a ground-proofed 6-cm resolution digital elevation model (DEM) derived from orthoimages captured from a drone flight on 10 February 2016. Because no major geomorphological changes occurred within the floodplain during the study period, we used the same DEM for all simulations for the four sampling events. The dimensions of the model mesh were chosen so as to minimize computation time and allow for

an accurate representation of flow-paths within the floodplain (Table S4, Supporting Information). We used measurements of substrate size distributions in the following equation (1) (Meyer-Peter and Müller 1948) to estimate  $k_{str}$ , the initial Strickler coefficient for bottom friction:

$$k_{str} = \frac{21.1}{\sqrt[6]{D_{90}}}$$

Because of the uncertainty surrounding this coefficient, it was then incrementally adjusted as part of the model calibration procedure. The upstream boundary condition for the model was the discharge value being modelled and the downstream boundary was a discharge-stage relationship. For model calibration, we used discharge and stage data for the period 13 March 2014 – 28 October 2016 from an automated gauging station at the downstream end of the modelling domain. Given the flashy nature of floods in the Maggia (typical flood duration <1day), no measurements of discharge-inundation relationships were made available, thus used a single gauge for calibration. The calibration to a single stream gauge was deemed robust, given the high vertical resolution of the bathymetry data and the fact that only one Strickler coefficient was used for the entire floodplain. The simulated stage-discharge relationship at the gauging station for each  $k_{str}$  value was compared with the measured one for the range of modelled floods and  $k_{str}$  was sequentially adjusted to minimize the root mean square error (RMSE). During the modelling period, 45 floods occurred, with a minimum discharge of 20.1 m<sup>3</sup>/s, a maximum of 570 m<sup>3</sup>/s, and average of 141.2 m<sup>3</sup>/s and standard deviation 164.8.

**Habitat characterization-** To summarize the physico-chemical attributes within each habitat, we performed a principal component analysis on selected physico-chemical variables after removing variables with Pearson's correlation greater than 0.7; variables included were nitrate concentration, electrical conductivity, dissolved oxygen (DO), mean water temperature (T) and standard deviation of water temperature.

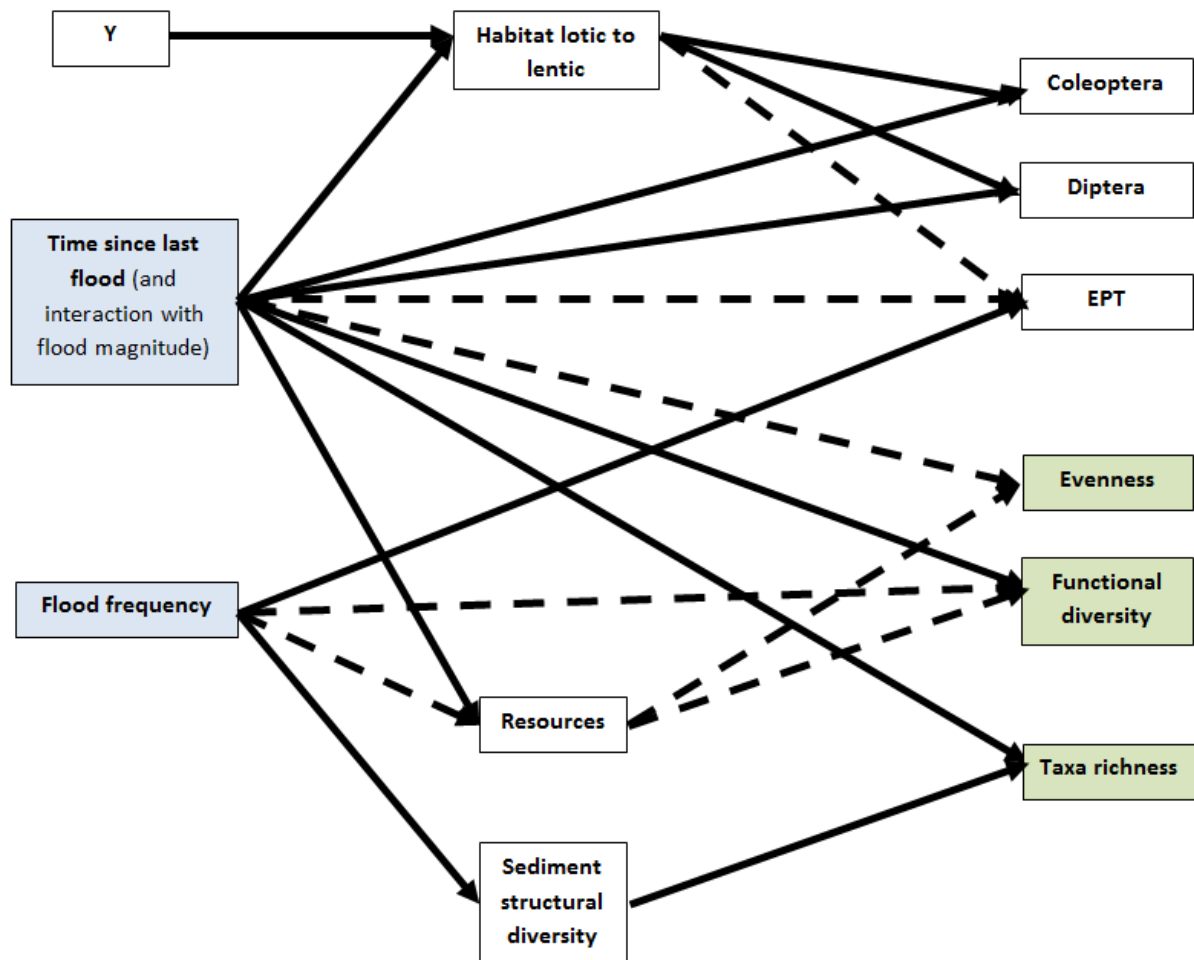
### *Statistical analysis*

We conducted a STATICO analysis to explore the relationship between macroinvertebrate community composition and environmental variables during the study period. STATICO is a three-way analysis coupling method designed to analyse the relationships between two series of tables: in our case a temporal series of environmental variables and one temporal series of species abundance data (Simier et al. 1999, Thioulouse et al. 2004, Thioulouse 2011, Slimani et al. 2017). Its usefulness in characterizing environment-biota relationships over time has been demonstrated in several studies (Carassou and Ponton 2007, Simier et al. 2006, Mendes et al. 2009).

We used piecewise structural equation modelling (SEM) to assess the direct and indirect effects of flood regime and history on macroinvertebrates. SEMs are adapted to model direct and indirect correlations in ecological systems while accounting for residual correlations between response variables (Bollen 1989, Grace et al. 2006). Piecewise SEMs differ from traditional SEMs in that instead of a variance-covariance matrix, they rely on local estimates to infer direct and indirect pathways (Grace et al. 2012, Pasanen-Mortensen et al. 2013). Because piecewise SEMs combine the information of multiple separate models into a causal framework, they allow for the use of random effects and release some of the assumptions made by traditional SEMs; they also accommodate smaller sample sizes. All pathways in the model were modelled using linear mixed effect models from the *lme* R package and combined into a structural model using the PiecewiseSEM R package (Lefcheck et al. 2016). Because of the repeated-measure structure of our dataset, we used site ID as a random effect in all models to account for



unmeasured site-specific effects, and the season of each sampling event was included as fixed factor in each model to correct for seasonal effects. Following Grace et al. (2006, 2012), we



constructed an initial conceptual structural model based on literature and a priori knowledge on the functioning of alluvial floodplain systems (Figure 4).

**Figure 4.** Initial structural equation model corresponding to our a priori conceptual understanding of the system. Plain arrows represent positive correlations and dashed arrows represent negative correlations.

We then optimized this model using a stepwise backward selection procedure based on the AICc criterion for each separate GLMM (Pasanen-Mortensen et al. 2013, Theodorou et al. 2016). Based on the d-separation test implemented in the PiecewiseSEM package, we incrementally incorporated significant missing pathways that further improved the AICc of the overall model (Stenegren et al. 2017, Shipley et al. 2009, Shipley et al. 2013). The final model was the one with the lowest AIC and the most variables (Stenegren et al. 2017).

#### *Model justification, with predicted responses*

The original model was developed to be associated with our initial hypotheses with a summary of rationale or justification presented in Table 1. Specifically, to test H1 (see introduction) we included negative correlations between the habitat gradient (lotic to lentic) and

both the time since last flood and the Y coordinate. To test H2, we initially assumed that the relative abundances of Coleoptera and Diptera would be positively correlated to the habitat gradient and to the time since last flood, whereas the relative abundance of EPT taxa would be negatively correlated to these variables. To test H3, we initially included a negative correlation between biofilm biomass and flood frequency and a positive one between biofilm biomass and time since last flood. Finally, to test H4, we assumed that functional diversity and community evenness would be negatively correlated to biofilm biomass. We also tested whether taxa richness increased over time after flood, and whether it was higher in frequently flooded habitats because of higher structural diversity in the substrata. To that end we included a positive correlation between taxa richness and time since last flood, as well as a positive correlation path between flood frequency, sediment structural diversity and taxa richness.

**Table 1.** Justification and rationale for the initial structural equation mode

Justification	Response	Driver	Sign	References	
Upwelling of groundwater in downstream reaches of the Maggia floodplain	Conductivity Nitrate	Y coordinate (increase downstream)	↗ ↗	Ruf et al. 2008, Larned and Datry 2013	
Mixing of waters during flood, homogenization with main stem	DO Conductivity	Time since flood	↗ ↗	Paillex et al. 2009	
Habitats become more isolated from surface and groundwater sources over time	Mean Temperature SD Temperature		↗ ↗	Rostan et al. 1987, Schwartz et al. 1996	
All above relationships result in a general habitat gradient	Habitat gradient lotic to lentic	Time since last flood AND Y coordinate	↗		
Biofilm grows over time after being reset by the flood	Biofilm	Time since flood	↗	Biggs and Close 1989, Tockner et al. 1999, Tockner et al. 2000, Ahearn et al. 2006	
The mechanical effect of floods tend to increase substrate heterogeneity	Substrate structural diversity	Flooding frequency	↗	Bornette and Amoros 1996	
Direct removal of individuals, followed by recolonization	Taxa richness	Time since flood	↗	Matthaei et al. 1997, 1999	
More ecological niches available with more diverse habitat structure		Structural diversity of habitat	↗	Brunke et al. 2003	
Floods enable EPT taxa to readily disperse from the main stem where they abound. EPT are generally good aerial dispersers and therefore recolonize faster from adjacent patches after flood.	EPT relative abundance	Time since flood	↘	Alp et al.2012	
EPT taxa are generally sensitive with a preference for lotic floodplain habitats		Flooding frequency	↗		Brunke et al. 2003
		Habitat lotic to lentic	↘		
Coleoptera and Diptera taxa are generally tolerant taxa with a preference for lentic floodplain habitats	Coleoptera and Diptera relative abundances	Time since flood Habitat lotic to lentic	↗ ↗	Brunke et al. 2003	
Competitive interactions and therefore functional diversity should increase over time after flood	Functional Diversity	Time since flood	↗	Fairchild et al. 2000, Mouquet et al. 2003, Cadotte 2017 Townsend et al. 1997, Gallardo et al. 2009, Paillex et al. 2013	
Functional diversity should be highest in rarely flooded habitats as a result of competitive interactions, short study duration is not expected to allow competitive exclusions		Flooding frequency	↘		
Low resource availability should favour interspecific competition and therefore lead to an increase in functional diversity.			Benthic primary productivity	↘	Passy et al. 2017
The high interspecific competition at low resource availability should cause a decrease in community evenness as stronger competitors outgrow others.	Community Evenness	Benthic primary productivity	↗		
Evenness should also be lowest in rarely flooded habitats as a result of competitive interactions			Flooding frequency	↗	Townsend et al. 1997, Gallardo et al. 2009, Paillex et al. 2013
			Time since flood	↘	

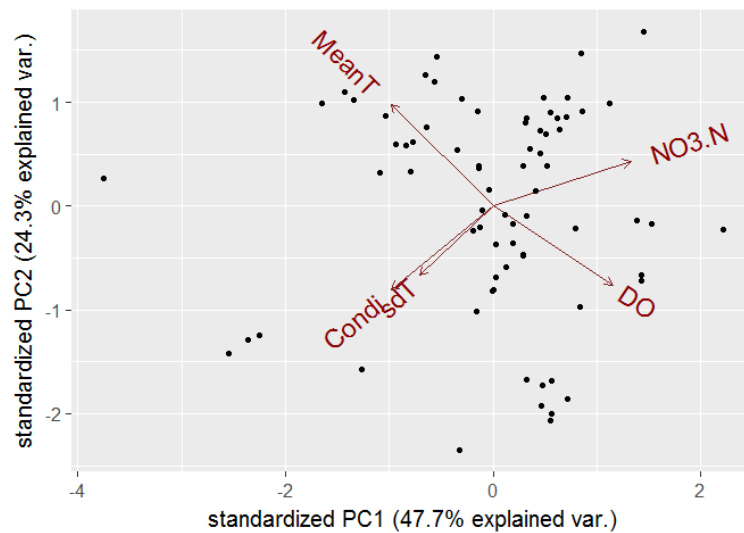
## Results

### *Hydrodynamic model*

After calibration, the hydrodynamic model was able to accurately reproduce water depth at the gauging station (Figure S1, Supporting Information) for the range of modelled discharges with a  $k_{str} = 26$ . Equation (1) resulted in an initial value of 25 for  $k_{str}$ , this value was then changed by increments of 1 unit until a minimum RMSE was reached for all range of discharges. RMSE ranged from 0.14, 0.10, 0.07, 0.046, 0.047 for  $k_{str} = 23, 24, 25, 26$  and 27, respectively. The  $k_{str}$  value of 26 gave the lowest RMSE among all tested values (0.046) and was therefore retained as the final friction parameter for the simulation of floodplain inundation. Discharge threshold values for habitat inundation ranged from 10 to 250  $m^3/s$  (mean = 49  $m^3/s$ , median = 35  $m^3/s$ , standard deviation = 58  $m^3/s$ ). Flood frequency for the different parafluvial habitats ranged from 0.52 to 18.04 floods per year (Table S5, Supporting Information). Time elapsed since the last flood varied greatly among habitats at each date, owing to the wide range of inundation thresholds (Table S5, Supporting Information).

### *Habitat characteristics*

The range of values in abiotic attributes indicated that the parafluvial habitats we selected in the floodplain were environmentally heterogeneous (Table S6, Supporting Information). PCA1 explained 48% of the total variation in physico-chemistry and therefore was used as indicator for “habitat” type in subsequent analyses (Figure 5).



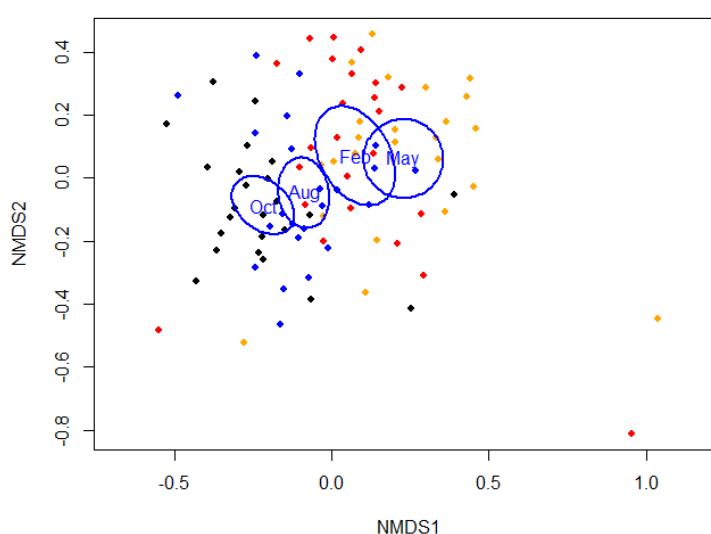
**Figure 5.** Plot of the PCA performed on the variables: mean water temperature (Mean T, °C), standard deviation of water temperature (SD T, °C), dissolved oxygen (DO, mg/l), nitrate concentration (NO<sub>3</sub>.N, mg/l) and electrical conductivity (Condi. µS/cm).

PCA1 was primarily structured by the opposition between habitats with high DO and nitrate concentration on the positive side, and habitats with high and variable average water

temperatures as well as high electrical conductivity on the negative side (Table S7, Supporting Information).

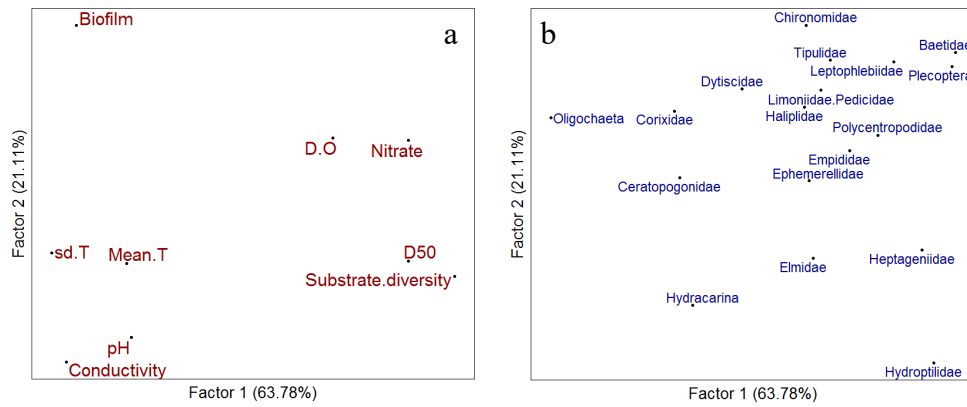
### *Community composition*

A total of 18 taxa were collected during the surveys, including species of Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, Diptera, Heteroptera, Hydracharina, and Oligochaeta (Table S8, Supporting Information). Taxa richness changed little between seasons, it was lowest in February (10.9 taxa), then increased in May and August (11.1 and 11.5 taxa, respectively) and decreased in October (11.4 taxa). Macroinvertebrate density varied through time with 338 individuals/sample in February to 140 in May, 271 in August and 317 in October. Despite these temporal changes in abundances, there was little variation in community composition among seasons (Figure 6).



**Figure 6.** NMDS plot showing the composition of the macroinvertebrate communities at each sampling date; ellipses are 95% confidence intervals.

STATICO analysis showed that relationships between environmental variables and community composition were significant at all four dates ( $p$  values = 0.024, 0.006, 0.005 and 0.017 for February, May, August and October, respectively). The first axis accounted for 63.8% of the explained variance and the second axis for 21.1%. Axis-1 was primarily structured by the opposition between habitats with high DO and nitrate concentrations as well as coarse and diverse substrata on the one side and habitats with warm and variable water temperatures as well as high electrical conductivity on the other (Figure 7a).

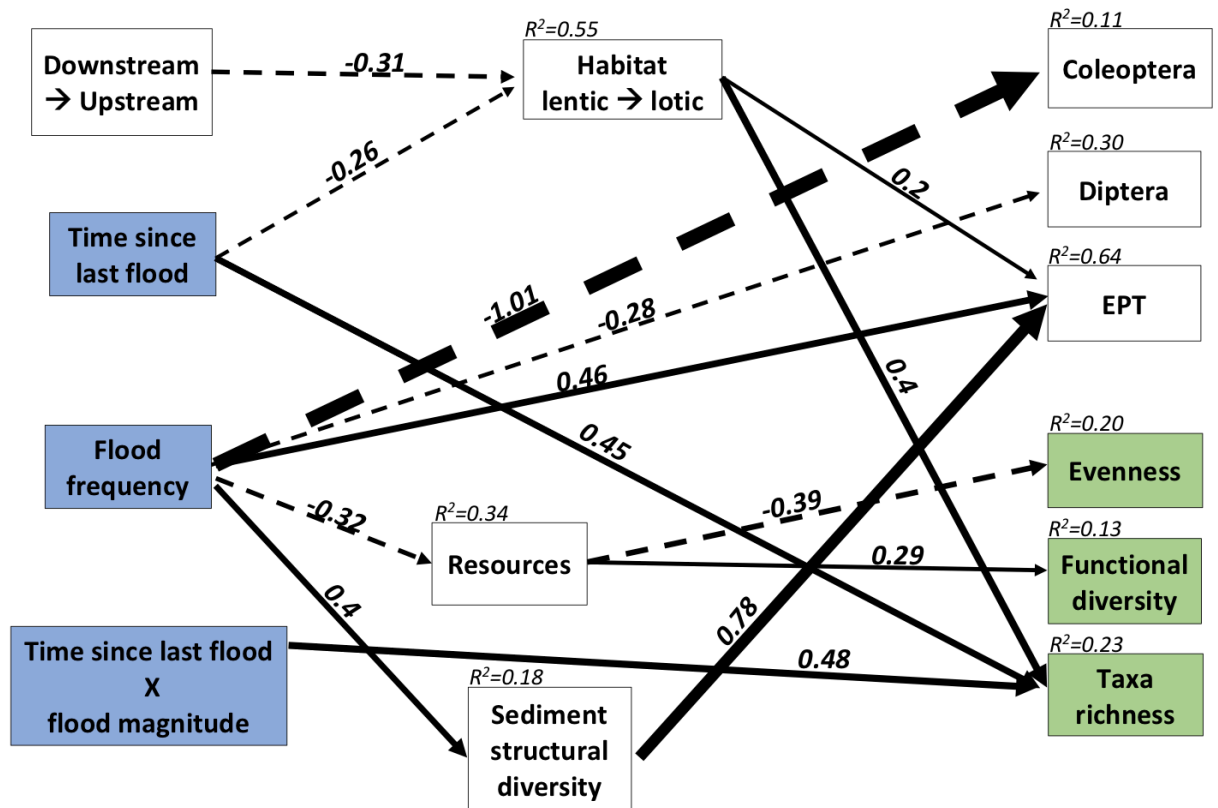


**Figure 7.** Plots showing the results of STATICO analysis. (a) principal axes showing the contributions of environmental variables, and (b) principal axes showing the invertebrate community composition.

This result can be interpreted as a gradient from lentic-like habitats on the left side to lotic-like habitats on the other. Axis-2 was mainly constrained by periphyton biomass in the different habitats. Further, the analysis of species distributions revealed that Oligochaete, Corixidae, Ceratopogonidae, Hydracarina and Dytiscidae dominated communities at more lentic habitats (right hand side), whereas EPT taxa were more abundant at habitats with more lotic attributes (Figure 7b). The linkage between environmental variables and community composition was stronger in August and May and weaker in October and February (Figure S2, Supporting Information).

#### *Piecewise SEM*

The piecewise SEM after stepwise optimization was well supported by the data (Fishers'C = 104.54,  $p = 0.175$ , Figure 8). According to the final SEM model, both the distance downstream along the floodplain (estimate = -0.31,  $p = 0.025$ ) and time elapsed since the last flood (estimate = -0.258,  $p = 0.035$ ) negatively affected the habitat gradient (PCA1). This result means that habitats located further downstream or not recently flooded had lower DO and nitrate concentrations and higher electrical conductivity than other habitats. These habitats also had warmer and more variable water temperatures. Because the habitat gradient was correlated positively to taxa richness (estimate = 0.494,  $p = 0.01$ ) and the proportion of EPT taxa (estimate = 0.265,  $p = 0.033$ ), these habitat conditions mediated the negative effects of the longitudinal location of habitats and time since last flood on these two variables. In contrast to the model, periphyton biomass was not affected by time since last flood or flood magnitude, but was negatively related to flood frequency (estimate = -0.324,  $p = 0.041$ ). Periphyton biomass was positively correlated to FD (estimate = 0.286,  $p = 0.037$ , Figure S3 Supporting Information), thus it mediated the negative effect of flood frequency on FD and the positive effect of flood frequency on community evenness through a negative correlation with this response variable (estimate = -0.386,  $p = 0.011$ ).



**Figure 8.** Final structural equation model after optimization. Plain arrows represent positive correlations and dashed arrows represent negative correlations and annotations on arrows show the strength of the relationships. R<sup>2</sup> values correspond to marginal R squares. The thicknesses of the arrows are scaled to the strength of the correlations.

Lastly, the relative abundance of Coleoptera and Diptera were negatively correlated to flood frequency (estimate = -1.01,  $p = 0.0387$ , estimate = -0.276,  $p = 0.04$ , respectively). Flood frequency had a positive effect on substrate diversity (estimate = 0.419,  $p = 0.0003$ ), which was positively correlated to the relative abundance of EPT taxa (estimate = 0.78,  $p = 0.022$ ). Taxa richness was positively correlated to the interactive term between time since last flood and flood magnitude (estimate = 0.485,  $p = 0.02$ , Figure S4, Supporting Information).

## Discussion

In this study, we examined the relative effects of long-term flood frequency and time since the last flood on macroinvertebrate communities in 24 parafluvial habitats. We sampled habitats seasonally over one year and used a combination of 2D hydrodynamic modelling and piecewise SEM to quantify direct and indirect effects of local hydrological metrics on community composition, taxa evenness, taxa richness and functional diversity. Importantly, we found that high flood frequency favoured rheophilic species (EPT taxa) over more lentic groups (Coleoptera, Diptera) and limited strong competitive interactions and competitive exclusion to occur by maintaining low periphyton standing crops. Further, we found that habitat characteristics became more lentic-like as time passed after a flood. This relationship caused EPT taxa to be relatively more abundant and taxa richness higher immediately after flood disturbance, although taxa richness increased over time after a flood and even more so after large floods.

*Local conditions are affected by recent disturbance history and flood regime*

The resulting hydrodynamic model accurately reproduced the stage-discharge relationship for the range of discharges considered. The single-value calibration of the bottom friction parameter was justified in this case, for only open gravel areas were flooded at the discharges considered and the spatial distribution of substrate size was relatively homogeneous. The wide range of modelled discharge thresholds for inundation of different parafluvial habitats reflected the geomorphological complexity of the floodplain. This heterogeneity also was apparent in the flood frequency values and time since last flood. The high average time since last flood in February reflected the glacial flow regime of the catchment; precipitation mainly falls as snow in the headwaters during winter, resulting in stable low flows. In contrast, the intermediate but variable values for time since last flood in May and August (median 24 and 63 days, respectively) together with high standard deviations (120 and 123, respectively) showed that medium-sized floods occurred during spring and summer, affecting some habitats but not others. Lastly, the low median time since last flood (5 days) in October showed that a large flood recently inundated most parafluvial habitats.

STATICO analysis revealed that the lotic to lentic habitat gradient had a strong effect on community composition, with more rheophilic EPT taxa predominantly occurring in the more lotic habitats. Temporal fluctuations in the strength of this environment-biota linkage (weaker linkage during winter and autumn compared to summer and spring) reflected the lower heterogeneity in habitat conditions in the floodplain in autumn and winter. Conversely, habitat conditions diverged more during spring and summer and the filtering effect on communities also was stronger. Results of this exploratory analysis confirmed that the environmental variables chosen to represent the effect of habitat type on communities in the subsequent SEM was adequate.

As expected, physico-chemical characteristics of floodplain habitats were strongly affected by their location along the longitudinal axis, with habitats further downstream (lower Y coordinate) exhibiting more “groundwater-dominated” waters with more stable and colder temperatures and high nutrient levels. Importantly, these differences in physico-chemical attributes were not solely explained by water origin, but also by the stage of succession a given habitat was at (Amoros and Bornette 2002, Thomaz et al. 2007). For instance, high DO levels are unlikely to be caused by groundwater inputs because the degradation of organic compounds in groundwater typically results in low DO levels. Instead, the negative relation of time since last flood on PCA axis-1 provided a parsimonious explanation to this pattern, confirming H<sub>1</sub>. DO levels rose during floods with the influx of well-oxygenated river water, and remained high immediately after floods. As a habitat became disconnected from the main channel, biological processes consumed oxygen causing a decrease in DO levels over time. To summarize, a parafluvial habitat tends to be better oxygenated if recently flooded, and cooler and thermally more stable if receiving inputs of groundwater.

The decrease in substrate structural diversity with increasing flood frequency likely resulted from geomorphological differences among habitats, where least flooded habitats were at a higher elevation compared to the river channel. Typically, these areas are zones of deposition and accumulation of smaller sized sediment during floods. This result was confirmed by the positive correlation between the Shannon index of structural diversity and median particle diameter ( $r = 0.67$ ).



Counter to hypothesis H<sub>4</sub>, periphyton biomass did not increase over time after a flood, but decreased with increasing flooding frequency. This direct effect suggests that periphyton levels remained low due to frequent flood disturbance (e.g., scouring). Another likely explanation is that high EPT abundance, especially mayflies, at regularly flooded habitats also kept biofilm standing crops to low levels by grazing. Grimm and Fischer (1986) hypothesized that periphyton growth rates are controlled by ambient nutrient concentrations and that maximum standing crops are primarily constrained by flood frequency (also see (Biggs and Close 1989, Robinson and Minshall 1986).

*Community composition primarily responds to flood regime and local abiotic conditions*

Hypothesis H<sub>3</sub> stated that community composition would change overtime after flood disturbance, partly reflecting the dispersal ability of taxa, was only partially supported by the data and the final model. No direct effect of time since last flood on community composition was observed, suggesting that local environmental filtering or biotic interactions played a larger role in structuring communities than the dispersal ability of taxa. However, the significant relationship between habitat characteristics and the relative abundance of EPT taxa suggests their high dispersal ability enabled them to track favourable environmental conditions (Tonkin et al. 2016), partially supporting H<sub>3</sub>. Conversely, no relationship between habitat and the relative abundances of Coleoptera and Diptera suggests that the habitat gradient was too short to filter these species or that mass effects associated with very high dispersal rates overrode environmental constraints (Leibold et al. 2004, Holyoak et al. 2005). Independent of environmental constraints and recent disturbance history, the lower relative abundances of Coleoptera and Diptera at frequently flooded habitats indicated that these taxa were affected by flooding to a greater extent than EPT taxa. This difference could result from the high flood resistance of EPT taxa or their ability to recolonize rapidly from other source habitats (McMullen et al. 2012, Alp et al. 2012).

*Taxa richness increases as time passes after a flood, and more so after major floods*

We observed a linear increase in taxa richness over time after flooding (slope = 0.453), reflecting the temporal colonization of disturbed habitats by new species. The pattern of low richness post flood and recovery over time has been observed in many aquatic systems (Matthaei et al. 1997, Rader et al. 2007, Mundahl et al. 2011, Robinson 2012). The immediate decrease in taxa richness after a flood results from the physical removal of individuals, either by drifting or crushing, and the filtering of species according to their morphological or behavioural adaptation to flooding (Lytle and Poff 2004). Similarly, the positive interaction between flood magnitude and time since last flood on taxa richness showed that the increase in taxa richness after a flood is faster for larger floods than for smaller floods. Because it is independent of local environmental conditions, this general pattern can be attributed to the direct physical effect of large floods on assemblages, where larger flood disturbances reset communities to earlier successional stages than smaller floods, resulting in a greater availability of ecological niches for colonization (Townsend et al. 1997, Robinson 2012). In contrast, direct recolonization from adjacent undisturbed substrate patches after small floods likely occurred before new species colonized from other habitats, resulting in similar taxa richness before and after small floods (Townsend et al. 1997, Francoeur et al. 1998, Matthaei et al. 1999, Robinson et al. 2003). Finally, high taxa richness at habitats with more optimal environmental conditions (positive PCA1) indicates that more taxa can live in these habitats in contrast to the other habitats containing more

‘tolerant’ species (Passy et al. 2017). This idea is supported by the low relative abundance of rheophilic EPT taxa at more lentic habitats (negative PCA1).

*Resource availability mediates the effect of flood frequency on community assembly rules*

The positive relationship between SES Rao’s Q and periphyton biomass suggested that limiting similarity processes associated with strong competitive interactions was a primary assembly rule at habitats with high resource availability, whereas environmental filtering by local abiotic conditions dominated habitats with low resource availability (further inferred by a negative functional diversity). This result was in accordance with hypothesis H<sub>5</sub>. While this pattern may at first seem contrary to the expectation that competition would be stronger in habitats with low resources (Passy et al. 2017), these less productive habitats may instead exert a strong selective pressure on taxa through their mode of resource acquisition for instance (Bernard-Verdier et al. 2012).

The high community evenness in low resource habitats further suggested that no particular group of species was able to outcompete others. At high resource availability, low community evenness indicated that some taxa were able to outcompete others and dominate assemblages, as reflected in the higher functional diversity indicative of strong competitive interactions (Cotgreave and Harvey 1994, Hillebrand et al. 2007, Zhang et al. 2006, Gamfeldt et al. 2011, Larpkern et al. 2011). However, the lack of relationship between resource availability and the relative abundance of a particular taxon suggested that the identity of these dominant competitors differed between sites and thus largely constrained by stochastic processes (Tilman et al. 2004) or driven by site-specific external factors. It is likely that this study did not cover the full range of habitat conditions (higher resource availability) or time period (lower flood frequency) that favours interspecific competition because the outcome of such strong competition would likely be extirpation of poor competitors (Townsend et al. 1997), a reduction in functional diversity, and a potential increase in evenness (Paillex et al. 2013, Kraft et al. 2015, Cadotte et al. 2017).

Previous studies investigating functional diversity in floodplain macroinvertebrate communities found that FD peaked at intermediate levels of inundation frequency, being lower at low and high inundation frequencies (Gallardo et al. 2009, Paillex et al. 2013). These findings are in line with predictions of the intermediate disturbance hypothesis (e.g., Townsend et al. 1997) and dynamic equilibrium model (Huston 1979, 1994). Taken together, these concepts suggest that at high flood frequency and low resource availability, strong environmental filtering can occur, notably on species resistance to floods and respective dispersal capacities. In contrast, strong competitive interactions and potentially competitive exclusion can develop in rarely flooded, highly productive habitats. Many studies have documented these colonization-competition trade-offs, where frequently disturbed habitats favour strong dispersers able to rapidly colonize recently disturbed patches and track favourable environmental conditions (Cadotte et al. 2007, Leibold et al. 2004, Soininen 2014, Tonkin et al. 2016), whereas strong competitors dominate community composition later in the assembly (Fairchild 2000, Mouquet et al. 2003, Cadotte et al. 2007).

In this study, the level of flood disturbance was negatively correlated to resource availability (periphyton biomass), which affected the relative importance of competition and environmental filtering. Our findings are in accordance with the predictions of Huston (1979 and 1994), Townsend et al. (1997) and Ward et al. (1999), in that low flood frequency at habitats

with high resource availability did not limit the development of strong competitive interactions, whereas the combination of high flood-disturbance frequency and low resource availability acted as a strong environmental filter on assemblages. Overall, our findings showed that high flood frequency maintained low periphyton biomass levels and limited the development of strong competitive interactions (as shown by high positive FD) and competitive exclusion to occur (as shown by decreasing community evenness).

#### *Implications for management: hydrological regime and floodplain biodiversity*

Our findings, as discussed above, have direct implications for the management of river flow regimes and the conservation of biodiversity in alluvial floodplain systems. First, spatial heterogeneity in flood frequencies should be maintained to provide ecological niches among parafluvial habitats for both lotic and lentic species within floodplain riverscapes. In order to achieve this spatial heterogeneity in flood frequencies, habitats should differ in their connectivity (e.g., elevation differences) with the main channel and floods should differ in magnitude. This heterogeneity will sustain a spatial mosaic of habitat patches with differing resource availability. In more productive habitats, strong competitive interactions will emerge and strong competitors will tend to outcompete others, thus reducing local diversity but increasing beta diversity. Second, independent of long-term flood frequency, a high level of heterogeneity in flood return period should be maintained among parafluvial habitats. This heterogeneity would result in a mosaic of habitat successional stages, further enhancing macroinvertebrate beta diversity at the floodplain scale. Additionally, high heterogeneity in disturbance states among parafluvial habitats can act as ‘spatial’ insurance for ecosystem functioning and stability of floodplain riverscapes (Loreau et al. 2003). Finally, large floods also should be maintained, for they allow regeneration of ecological niches and colonization by novel taxa, thereby sustaining high taxa richness in floodplains.

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## **References**

- Ahearn D. S., Viers, J. H., Mount, J. F. and Dahlgren, R. A. 2006. Priming the productivity pump: flood pulse driven trends in suspended algal biomass distribution across a restored floodplain. *Freshwater Biology*, 51: 1417-1433.
- Alp, M., Keller, I., Westram, A. M. and Robinson, C. T. 2012. How river structure and biological traits influence gene flow: a population genetic study of two stream invertebrates with differing dispersal abilities. *Freshwater Biology*, 57: 969-981
- Amoros, C., and Bornette, G. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology* 47: 761-776.

- Arscott, D. B., Tockner, K., and Ward, J.V. 2003. Spatio-temporal patterns of benthic invertebrates along the continuum of a braided Alpine river. *Archiv für Hydrobiologie* 4: 431-460
- Arscott, D. B., Tockner, K., Van der Nat, D., and Ward, J. V. 2002. Aquatic Habitat Dynamics along a Braided Alpine River Ecosystem (Tagliamento River, Northeast Italy). *Ecosystems* 5:802-814
- Bernard-Verdier, M., Navas, M., Vellend, M., Violle, C., Fayolle, A., Garnier, E. and Cornelissen, H. 2012. Community assembly along a soil depth gradient: contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. *Journal of Ecology* 100: 1422-1433
- Bevenger G.S., and King RM. 1995. A pebble count procedure for assessing watershed cumulative effects. RM-RP-319. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO.; 17.
- Biggs, B. J. and Close, M. E. 1989. Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biology*, 22: 209-231
- Bollen, K. A. 1989. A New Incremental Fit Index for General Structural Equation Models. *Sociological methods and Research* 17:303-316
- Bond N. R., and Downes B. J. 2000. Flow-related disturbance in streams: an experimental test of the role of rock movement in reducing macroinvertebrate population densities. *Marine and Freshwater Research* 51, 333-337.
- Borchardt, D. 1993. Effects of flow and refugia on drift loss of benthic macroinvertebrates: implications for habitat restoration in lowland streams. *Freshwater Biology*, 29: 221-227.
- Bornette, G. and Amoros, C. 1996. Disturbance regimes and vegetation dynamics: role of floods in riverine wetlands. *Journal of Vegetation Science*, 7: 615-622
- Brunke, M., Hoehn, E., and Gonser, T. 2003. Patchiness of River–Groundwater Interactions within Two Floodplain Landscapes and Diversity of Aquatic Invertebrate Communities. *Ecosystems* 6: 707-722.
- Burnett, M. R., August, P. V., Brown, J. H., and Killingbeck, K. T. 1998. The Influence of geomorphological heterogeneity on biodiversity: a patch-scale perspective. *Conservation Biology*, 12: 363-370.
- Cadotte, M. W. 2007. Competition-colonization trade-offs and disturbance effects at multiple scales. *Ecology* 88:823- 829. Doi: 10.1890/06-1117
- Capderrey, C., Datry T., Foulquier, A., Claret, C. and Malard, F. 2013. Invertebrate distribution across nested geomorphic features in braided-river landscapes. *Freshwater Science* 32: 1188–1204. doi: 10.1899/12-188.1
- Carassou, L., and Ponton, D. 2007. Spatio-temporal structure of pelagic larval and juvenile fish assemblages in coastal areas of New Caledonia, southwest Pacific. *Marine Biology* 150: 697-711. doi: 10.1007/s00227-006-0389-y
- Cellot, B., Dole-Olivier, M. J., Bornette, G. and Pautou, G. 1994. Temporal and spatial environmental variability in the Upper Rhône River and its floodplain. *Freshwater Biology*, 31: 311-325. Doi: 10.1111/j.1365-2427.1994.tb01743.x
- Chang, C., and HilleRisLambers, J. 2016. Integrating succession and community assembly perspectives. *F1000Research*, 5, F1000 Faculty Rev–2294. Doi: 10.12688/f1000research.8973.1

- Coops, H., Tockner, K., Amoros, C., Hein, T., and Quinn, G. 2006. Restoring lateral connections between rivers and floodplains: lessons from rehabilitation projects. *Wetlands and Natural Resource Management* (eds J.T.A. Verhoeven, B. Beltman, R. Bobbink and D.F. Whigham), pp. 15–32. Springer, Berlin, Germany.
- Cornwell, W. K. and Ackerly, D. D. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, 79: 109-126. Doi: 10.1890/07-1134.1
- Cotgreave, P. and Harvey, P. 1994. Evenness of Abundance in Bird Communities. *Journal of Animal Ecology*, 63: 365-374. Doi: 10.2307/5554
- Datry, T., Corti, R., Belletti, B. and Piégay, H. 2014. Ground-dwelling arthropod communities across braided river landscape mosaics: a Mediterranean perspective. *Freshwater Biology*, 59: 1308-1322. Doi: 10.1111/fwb.12350
- Diaz, S., and Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in ecology and Evolution* 11: 646-655. Doi: 10.1016/S0169-5347(01)02283-2
- Diaz, S., Cabido, M. and Casanoves, F. 1999. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* 9: 113–122. Doi: 10.2307/3237229
- Faeh, R., Mueller, R., Rousselot, P., Veprek, R., Vetsch, D. and Volz, C. 2010. "BASEMENT - Basic Simulation Environment for Computation of Environmental Flow and Natural Hazard Simulation." Software Manual. VAW, ETH Zurich ([www.basement.ethz.ch](http://www.basement.ethz.ch)).
- Fairchild, G. W., Faulds, A. M. and Matta, J. F. 2000. Beetle assemblages in ponds: effects of habitat and site age. *Freshwater Biology* 44: 523-534. Doi: 10.1046/j.1365-2427.2000.00601.x
- Fernandes, I. M., Henriques-Silva, R., Penha, J., Zuanon, J., and Peres-Neto, P. R. 2014. Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities. *Ecography* 37: 464-475. Doi: 10.1111/j.1600-0587.2013.00527.x
- Fernandes, I. M., Henriques-Silva, R., Penha, J., Zuanon, J. and Peres-Neto, P. R. 2014. Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities. *Ecography* 37: 464-475. Doi: 10.1111/j.1600-0587.2013.00527.x
- Francoeur, S.N., Biggs, B.J.F. and Lowe, R.L. 1998. Microform bed clusters as refugia for periphyton in a flood-prone headwater stream. *New Zealand Journal of Marine and Freshwater Research*, 32: 363–374. Doi: 10.1080/00288330.1998.9516831
- Gallardo, B., Doledéc, S., Paillex, A., Arscott, D. B., Sgeldon, F., Zilli, F., Mérigoux, S., Castella, E. and Comin, F. A. 2014. Response of benthic macroinvertebrates to gradients in hydrological connectivity: a comparison of temperate, subtropical, Mediterranean and semiarid river floodplains. *Freshwater Biology* 59: 630-648. Doi: 10.1111/fwb.12292
- Gallardo, B., Garcia, M., Cabezas, A., Gonzalez, E., Gonzalez, M., Ciancarelli, C. and Comin, F. A. 2008. Macroinvertebrate patterns along environmental gradients and hydrological connectivity within a regulated river-floodplain. *Aquatic Sciences* 70: 248-258. Doi: 10.1007/s00027-008-8024-2
- Gallardo, B., Gascon, S., Cabezas, A., Gonzalez, M., Garcia, M. and Comin, F.A. 2009. Relationship between invertebrate traits and lateral environmental gradients in a

- Mediterranean river-floodplain. *Fundamental and Applied Limnology*, 173, 281–292. Doi: 10.1127/1863-9135/2009/0173-0281
- Gamfeldt L, Hillebrand H. 2011. Effects of Total Resources, Resource Ratios, and Species Richness on Algal Productivity and Evenness at Both Metacommunity and Local Scales. *PLOS ONE* 6(7). Doi: 10.1371/journal.pone.0021972
- Gibbins, C., Batalla, R. J. and Vericat, D. 2010. Invertebrate drift and benthic exhaustion during disturbance: Response of mayflies (Ephemeroptera) to increasing shear stress and river-bed instability. *River Res. Applic.*, 26: 499-511. Doi: 10.1002/rra.1282
- Gibbins, C., Vericat, D. and Batalla, R. J. 2007. When is stream invertebrate drift catastrophic? The role of hydraulics and sediment transport in initiating drift during flood events. *Freshwater Biology* 52: 2369-2384. Doi: 10.1111/j.1365-2427.2007.01858.x
- Gorski, K., Collier, K. J., Duggan, I. C., Taylor, C. M. and Hamilton, D. P. 2013. Connectivity and complexity of floodplain habitats govern zooplankton dynamics in a large temperate river system. *Freshwater Biology* 58: 1458-1470. Doi: 10.1111/fwb.12144
- Grace, J. B. and Keeley, J. E. 2006. A Structural Equation Model Analysis Of Postfire Plant Diversity In California Shrublands. *Ecological Applications*, 16: 503-514. Doi: 10.1890/1051-0761(2006)016[0503:ASEMAO]2.0.CO;2
- Grace, J. B., Schoolmaster Jr., D. R., Guntenspergen, G. R., Little, A. M., Mitchell, B. R., Miller, K. M., and Schweiger, E. W. 2012. Guidelines for a graph-theoretic implementation of structural equation modeling. *Ecosphere* 3:73. Doi: 10.1890/ES12-00048.1
- Grimm, B., and fisher, S. G. 1986. Nitrogen limitation in a Sonoran Desert stream. *J. N. Am. Benthol. Soc.* 5: 2-15. Doi: 10.2307/1467743
- Hillebrand, H. Bennett, D. M. and Cadotte, M. W. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology*, 89: 1510-1520. Doi: 10.1890/07-1053.1
- Holyoak, M., Leibold, M. A., Mouquet, N. M., Holt, R. D., and Hoopes, M. F. 2005. Metacommunities - A framework for large-scale community ecology. - *Metacommunities: Spatial Dynamics and Ecological Communities*: 1–31.
- Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* 113: 81–101. Doi: 10.1086/283366
- Huston, M.A. 1994. *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge University Press, New York.
- Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Pages 110–127 in D. P. Dodge (ed.), *Proceedings of the international large river symposium (LARS)*. Canadian Journal of Fisheries and Aquatic Sciences Special Publication 106.
- Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of vegetation science* 3: 157-164. Doi: 10.2307/3235676
- Kraft, N. J. B., Godoy, O., and Levine, J. M. 2015. Plant functional traits and the multidimensional nature of species coexistence. *PNAS* 112: 797-802. Doi: 10.1073/pnas.1413650112
- Kuhn, N. and R. Amiet. 1988. *Bundesinventar der Auengebiete von Nationaler Bedeutung*, Eidg. Dep. Inners, Bundesamt fuer For. und Landschaftschutz, Abt. Natur und Heimatschutz, Bern, Switzerland.

- Larned, S. T., and Datry, T. 2013. Flow variability and longitudinal patterns in parafluvial water chemistry, aquatic invertebrates and microbial activity. *Freshwater Biology* 58: 2126-2143. Doi: 10.1111/fwb.12196
- Larpkern, P., Totland, Ø. and Moe, S. R. 2011. Do disturbance and productivity influence evenness of seedling, sapling and adult tree species across a semi-deciduous tropical forest landscape? *Oikos*, 120: 623-629. Doi: 10.1111/j.1600-0706.2010.18967.x
- Lefcheck, J. S. and Freckleton, R. 2016. PIECEWISESEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution* 7: 573-579. Doi: 10.1111/2041-210X.12512
- Leibold, M., A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J., B., Law, R., Tilman, D., Loreau, M. and Gonzalez, A. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7: 601-613. Doi: 10.1111/j.1461-0248.2004.00608.x
- Li, S., Cadotte, M. W., Meiners, S. J., Hua, Z., Jiang, L., and Shu., W. 2015. Species colonisation, not competitive exclusion, drives community overdispersion over long-term succession. *Ecology Letters* 18: 964-973. Doi: 10.1111/ele.12476
- Loreau, M., Mouquet, N., and Gonzalez, A. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. *PNAS* 100: 12765-12770. Doi: 10.1073/pnas.2235465100
- Lytle, D. A., and Poff, N L. 2004. Adaptation to natural flow regime. *Trends in ecology and evolution* 19:94-100. Doi: 10.1016/j.tree.2003.10.002
- MacArthur, R.H., and Levins, R. 1967. Limiting similarity convergence and divergence of coexisting species. *American Naturalist* 101: 377–385.
- Malard, F., Uehlinger, U. , Zah, R. and Tockner, K. 2006. Flood pulse and riverscape dynamics in braided glacial river. *Ecology*, 87: 704-716. Doi: 10.1890/04-0889
- Mason, N. W. H., de Belo, F., Mouillot, D., Pavoine, S., and Dray, S. 2013 A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science* 24: 794-806. Doi: 10.1111/jvs.12013
- Matthaei, C. D., Werthmüller, D., Frutiger, A. 1997. Invertebrate recovery from a bed-moving spate: the role of drift versus movements inside or over the substratum. *Archiv für Hydrobiologie* 140:221-235. Doi: 10.1127/archiv-hydrobiol/140/1997/221
- MCMullen, L. E. and Lytle, D. A. 2012. Quantifying invertebrate resistance to floods: a global-scale meta-analysis. *Ecological Applications*, 22: 2164-2175. Doi: 10.1890/11-1650.1
- Mendes, S., Fernandez-Gomez, M. J., Resende, P., Jorge Pereira, M., Purificación Galindo-Villardón, M., and Miranda Azeiteiro, U. 2009. Spatio-temporal structure of diatom assemblages in a temperate estuary. A STATICO analysis. *Estuarine, Coastal and Shelf Science* 84:637-644. Doi: 10.1016/j.ecss.2009.08.003
- Mérigoux, S., Forcellini, M., Dessaix, J. , Fruget, J. , Lamouroux, N. and Statzner, B. 2015. Testing predictions of changes in benthic invertebrate abundance and community structure after flow restoration in a large river (French Rhône). *Freshwater Biology* 60: 1104-1117. Doi: 10.1111/fwb.12422
- Meyer-Peter, E. and Müller, R. 1948. Formulas for Bed-Load transport. IAHSR, appendix 2, 2nd meeting:39–65.

- Meyns, S., R. Illi, and B. Ribi. 1994. Comparison of chlorophyll-a analysis by HPLC and spectrophotometry: Where do the differences come from? *Archiv für Hydrobiologie*, 132: 129–139
- Molnar, P.; Favre, Natalie; Perona, Paolo; Burlando, Paolo; Ruf, Wolfgang. 2008. Floodplain forest dynamics in a hydrologically altered mountain river. *Peckiana - Staatliche Museum für Naturkunde Goerlitz*, Vol. 5
- Mouquet, N., Munguia, P., Kneitel, J. M., and Miller, T. E. 2003. Community assembly time and the relationship between local and regional species richness. *Oikos* 103: 618-626. Doi: 10.1034/j.1600-0706.2003.12772.x
- Mouw, J. E., Chaffin, J. L., Whited, D. C., Hauer, F. R., Matson, P. L., and Stanford, J. A. 2013. Recruitment and successional dynamics diversify the shifting habitat mosaic of an Alaskan floodplain. *River Research and Applications* 29: 671-685. Doi: 10.1002/rra.2569
- Mundahl, N. D., and Hunt, A. M. 2011. Recovery of stream invertebrates after catastrophic flooding in southeastern Minnesota, USA, *Journal of Freshwater Ecology*, 26:4, 445-457. doi: 10.1080/02705060.2011.596657
- Opperman J. J., Luster, R., McKenney, B. A., Roberts, M., and Wrona Meadows, A. 2010. Ecologically functional floodplains: connectivity, flow regime and scale. *Journal of the American water resources association* 46: 211-226. Doi: 10.1111/j.1752-1688.2010.00426.x
- Paillex, A., Castella, E., and Carron, G. 2007. Aquatic macroinvertebrate response along a gradient of lateral connectivity in river floodplain channels. *Journal North American Benthological Society* 26: 779-796. Doi: 10.1899/06-12.1
- Paillex, A., Doledec, S., Castella, E., and Mériçoux, S. 2009. Large river floodplain restoration: predicting species richness and trait responses to the restoration of hydrological connectivity. *Journal of Applied Ecology* 46: 250-258. Doi: 10.1111/j.1365-2664.2008.01593.x
- Paillex, A., Doledec, S., Castelly, E., Mériçoux, S, and Aldridge, D. C. 2013. Functional diversity in a large river floodplain: anticipating the response of native and alien macroinvertebrates to the restoration of hydrological connectivity. *Journal of applied ecology* 50: 97-106. Doi: 10.1111/1365-2664.12018
- Pasanen-Mortensen, M., Pykönen, M. and Elmhagen, B. 2013. Where lynx prevail, foxes will fail – limitation of a mesopredator in Eurasia. *Global Ecology and Biogeography*, 22: 868-877doi: 10.1111/geb.12051
- Passy, S.I., Bottin, M., Soininen, J., and H. Hillebrand. 2017. Environmental filtering and taxonomic relatedness underlie the species richness–evenness relationship. *Hydrobiologia* 787: 787: 243. Doi: 10.1007/s10750-016-2968-3
- Perona, P., Camporeale, C., Perucca, E., Savina, M., Molnar, P., Burlando, P., and Ridolfi, L. 2009. Modelling river and riparian vegetation interactions and related importance for sustainable ecosystem management. *Aquat. Sci.*, 71: 266 – 278. Doi: 10.1007/s00027-009-9215-1
- Pfamatter, S. and P. Zanetta. 2003. Hydrogologie de la plaine alluviale du valmaggia entre bignasco et giomaglio (Tessin). Masters thesis, Universitt Lausanne.



- Rader, R. B., Voelz, N. J. and Ward, J. V. 2008. Post-Flood Recovery of a Macroinvertebrate Community in a Regulated River: Resilience of an Anthropogenically Altered Ecosystem. *Restoration Ecology*, 16: 24-33. Doi: 10.1111/j.1526-100X.2007.00258.x
- Robinson, C.T, and Minshall, G. W. 1986. Effects of Disturbance Frequency on Stream Benthic Community Structure in Relation to Canopy Cover and Season. *Journal of the North American Benthological Society* 5: 237-248. Doi: 10.2307/1467711
- Robinson, C. T. 2012. Long term changes in community assembly, resistance, and resilience following experimental floods. *Ecological Applications* 22: 1949-1961. Doi: 10.1890/11-1042.1
- Robinson, C.T., U. Uehlinger and M.T. Monaghan. 2003. Effects of a multi-year experimental flood regime on macroinvertebrates downstream of a reservoir. *Aquatic Sciences: Research Across Boundaries* 65:210-222. Doi: 10.1007/s00027-003-0663-8
- Rostan J.C., Amoros C. and Juget J. 1987. The organic content of the surficial sediment: a method for the study of ecosystems development in abandoned river channels. *Hydrobiologia*, 148, 45–62. Doi: 10.1007/BF00018165
- Ruf, W., L. Foglia, P. Perona, P. Molnar, R. Faeh, and P. Burlando (2008), Modeling the interaction between groundwater and river flow in an active alpine floodplain ecosystem, *Peckiana Staatl. Mus. Naturk. Goerlitz*, 5, 5–16
- Salo, J., Kalliola, R., Häkkinen, I., Mäkinen, Y., Niemela, P., Puhakka, M., and Coley, P.D. 1986. 'River dynamics and the diversity of Amazon lowland forests', *Nature*, 322, 254–258. Doi: 10.1038/322254a0
- Schwarz W.L., Malanson G.P. and Weirich F.H. 1996. Effect of landscape position on the sediment chemistry of abandoned-channel wetlands. *Landscape Ecology*, 11:27–38. Doi: 10.1007/BF02087111
- Scott, D. T., R. F. Keim, B. L. Edwards, C. N. Jones, and D. E. Kroes 2014. Floodplain biogeochemical processing of floodwaters in the Atchafalaya River Basin during the Mississippi River flood of 2011, *J. Geophys. Res. Biogeosci.*, 119, 537–546. Doi: 10.1002/2013JG002477
- Shipley B. 2009. Confirmatory path analysis in a generalized multilevel context. *Ecology* 90 363–368. 10.1890/08-1034.
- Shipley B. 2013. The AIC model selection method applied to path analytic models compared using a d-separation tests. *Ecology* 94 560–564. 10.1890/12-0976.
- Simier, M., Blanc L., Pellegrin, F., and Nandris, D. 1999. Approche simultanée de K couples de tableaux: application à l'étude des relations pathologie végétale – environnement *Revue de statistique appliquée*, 47 : 31-46
- Simier, M., Laurent, C., Ecoutin, J-M., Albaret, J-J. 2006. The Gambia River estuary: a reference point for estuarine fish assemblages studies in West Africa *Estuarine, Coastal and Shelf Science*, 69: 615-628. Doi: 10.1016/j.ecss.2006.05.028
- Slimani, N., Guilbert, E., Ayni, F.E., Jrad, A., Boumaiza, M., and Thioulouse, J. 2017. The use of STATICO and COSTATIS, two exploratory three-ways analysis methods: an application to the ecology of aquatic heteroptera in the Medjerda watershed (Tunisia). *Environmental and Ecological Statistics* 24: 269-295. Doi: 10.1007/s10651-017-0370-6

- Smith, R. F., Venugopal, P. D., baker, M. E., and Lamp, W. O. 2015. Habitat filtering and adult dispersal determine the taxonomic composition of stream insects in an urbanizing landscape. *Freshwater Biology* 60:1740-1754. Doi: 10.1111/fwb.12605
- Soininen, J. 2014. A quantitative analysis of species sorting accross organisms and ecosystems. *Ecology* 95: 3284-3292. Doi: 10.1890/13-2228.1
- Sommer, T., Harrell, B. , Nobriga, M. , Brown, R. , Moyle, P. , Kimmerer, W. and Schemel, L. 2001. California's Yolo Bypass: Evidence that flood control Can Be compatible with fisheries, wetlands, wildlife, and agriculture. *Fisheries*, 26: 6-16. Doi: 10.1577/1548-8446(2001)026<0006:CYB>2.0.CO;2
- Stanford J.A., Lorang M.S. and Hauer F.R. 2005. The shifting habitat mosaic of river ecosystems. *Verhandlungen des Internationalen Verein Limnologie*, 29, 123– 136. Doi: 10.1080/03680770.2005.11901979
- Starr, S., M., Benstead, J. P., Sponseller, R. A. 2014. Spatial and temporal organization of macroinvertebrate assemblages in a lowland floodplain ecosystem. *Landscape Ecology* 29: 1017-1031. Doi: 10.1007/s10980-014-0037-8
- Stenegren, M., Berg, C., Padilla, C. C., David, S.-S., Montoya, J. P., Yager, P. L., and Foster, R. A. 2017. Piecewise Structural Equation Model (SEM) Disentangles the Environmental Conditions Favoring Diatom Diazotroph Associations (DDAs) in the Western Tropical North Atlantic (WTNA). *Frontiers in Microbiology*, 8: 810. Doi: 10.3389/fmicb.2017.00810
- Stone M.C., Byrne C.F., and Morrison R.R. 2017. Evaluating the impacts of hydrologic and geomorphic alterations on floodplain connectivity. *Ecohydrology*10:e1833. Doi : 10.1002/eco.1833
- Tachet H., Bournaud M., Richoux P., and Usseglio-Polatera P. 2010: Invertébrés d'eau douce - systématique, biologie, écologie. CNRS Editions, Paris. Accessed through [www.freshwaterecology.info](http://www.freshwaterecology.info) - the taxa and autecology database for freshwater organisms, version 7.0 accessed on 23.02.2018.
- Theodorou P, Radzevičė R, Settele J, Schweiger O, Murray T.E., and Paxton R. J. 2016. Pollination services enhanced with urbanization despite increasing pollinator parasitism. *Proc. R. Soc. B*. Doi: 10.1098/rspb.2016.0561
- Thioulouse, J., Simier, M. and Chessel, D. 2004. Simultaneous analysis of a sequence of paired ecological tables. *Ecology*, 85: 272-283. Doi: 10.1890/02-0605
- Thioulouse, J. 2011. Simultaneous analysis of a sequence of paired ecological tables: a comparison of several methods. *The annals of applied statistics* 5:2300-2325. Doi: 10.1214/10-AOAS372
- Thomaz, S. M., Bini, L. M., and Bozelli, R. L. 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia* 579: 1-13. Doi: 10.1007/s10750-006-0285-y
- Thompson, R., and Townsend, C. 2006. A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. *Journal of Animal Ecology* 75: 476-484. Doi: 10.1111/j.1365-2656.2006.01068.x

- Tilman D. 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences* 101: 10854-10861. Doi: 10.1073/pnas.0403458101
- Tilman D. Functional diversity. 2001 In: Levin SA, editor. *Encyclopedia of Biodiversity*. Elsevier; Oxford: pp. 109–120.
- Tockner, K., Pusch, M., Borchardt, D., and Lorang, M. S. 2010. Multiple stressors in coupled river-floodplain ecosystems. *Freshwater Biology* 55:135-151. Doi: 10.1111/j.1365-2427.2009.02371.x
- Tockner, K., Malard, F. and Ward, J. V. 2000. An extension of the flood pulse concept. *Hydrol. Process.*, 14: 2861-2883. Doi: 10.1002/1099-1085(200011/12)14:16/17<2861::AID-HYP124>3.0.CO;2-F
- Tockner, K., Pennetzdorfer, D. , Reiner, N. , Schiemer, F. and Ward, J. V. 1999. Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river–floodplain system (Danube, Austria). *Freshwater Biology*, 41: 521-535. Doi: 10.1046/j.1365-2427.1999.00399.x
- Tockner, K. and Stanford, J. A. 2002. Riverine flood plains: present state and future trends. *Environmental Conservation* 29: 308–330. Doi: 10.1017/S037689290200022X
- Tockner, K., Malard, F., Burgherr, P., Robinson, C. T., Uehlinger, U., Zah, R., Ward, J. V. 1997. Physico-chemical characterization of channel types in a glacial floodplain ecosystem (Val Roseg, Switzerland). *Archiv für Hydrobiologie* 140: 433–463. Doi: 10.1127/archiv-hydrobiol/140/1997/433
- Tonkin, J., Stoll, S., Jähnig, S., and Hase, P. 2016. Contrasting metacommunity structure and beta diversity in an aquatic-floodplain system. *Oikos* 125: 686-697.
- Townsend C. R., Scarsbrook M. R. , Dolédec S. 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams, *Limnology and Oceanography*, 42: 938-949. Doi: 10.4319/lo.1997.42.5.0938
- Uehlinger, U. 1991. Spatial temporal variability of the periphyton biomass in a prealpine river (Necker, Switzerland). *Archiv für Hydrobiologie* 123: 219–237.
- Van Der Nat, D., Tockner, K. , Edwards, P. J., Ward, J. and Gurnell, A. M. 2003. Habitat change in braided flood plains (Tagliamento, NE-Italy). *Freshwater Biology*, 48: 1799-1812. Doi: 10.1046/j.1365-2427.2003.01126.x
- Van der Valk, A.G. 1981. Succession in wetlands: a Gleasonian approach. *Ecology* 62: 688–696. Doi: 10.2307/1937737
- Van der Vorste, R., Malard, F., and Datry, T. 2016. Is drift the primary process promoting the resilience of river invertebrate communities? A manipulative field experiment in an intermittent alluvial river. *Freshwater Biology* 61: 1276-1292. Doi: 10.1111/fwb.12658
- Ward, J., Tockner, K. , Schiemer, F. and Layzer, J. B. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regulated Rivers: Research and Management* 15: 125-139. Doi: 10.1002/(SICI)1099-1646(199901/06)15:1/3<125::AID-RRR523>3.0.CO;2-E
- Ward, J., Tockner, K. , Schiemer, F. and Layzer, J. B. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regul. Rivers: Res. Mgmt.*, 15: 125-139. Doi: 10.1002/(Sici)1099-1646(199901/06)15:1/3<125::Aid-Rrr523>3.0.Co;2-E

- Wentworth, C., K. 1922. A scale grade and class terms for clastic sediments. *The Journal of Geology*, 30:377-392. 10.1086/622910
- Whited, D. C., Lorang, M. S., Harner, M. J., Hauer, F. R., Kimball, J. S. and Stanford, J. A. 2007. Climate, hydrologic disturbance, and succession: drivers of floodplain pattern. *Ecology*, 88: 940-953. doi:10.1890/05-1149. Doi: 10.1890/05-1149
- Zhang, Q. and Zhang, D. 2006. Resource availability and biodiversity effects on the productivity, temporal variability and resistance of experimental algal communities. *Oikos*, 114: 385-396. Doi: 10.1111/j.2006.0030-1299.14723.x

## Supporting Information

**Table S1.** Wentworth substrate size classes

Size Code	Particle diameter range (mm)	Category
1	<0.062	silt/clay
2	0.062-0.125	very fine sand
3	0.125-0.25	fine sand
4	0.25-0.5	medium sand
5	0.5-1	coarse sand
6	1-2	coarse sand
7	2-4	fine gravel
8	4-5.7	medium gravel
9	5.7-8	medium gravel
10	8-11.3	coarse gravel
11	11.3-16	coarse gravel
12	16-22.6	small pebble
13	22.6-32	small pebble
14	32-45	large pebble
15	45-64	large pebble
16	64-90	small cobble
17	90-128	small cobble
18	128-180	large cobble
19	180-256	large cobble
20	256-362	boulder
21	362-512	boulder
22	512-1024	boulder
23	>1024	boulder
24	Bedrock	bedrock

**Table S2.** List of the 9 biological traits and the number of categories in each trait used to calculate the functional diversity of aquatic macroinvertebrates.

No.	Biological traits	Number of categories
1	Body size	5
2	Dispersal	4
3	Life duration	2
4	Reproduction	8
5	Locomotion	6
6	Aquatic stage	4
7	Feeding habits	6
8	Respiration technique	3
9	Voltinism	3

**Table S3.** Summary statistics of the 45 floods that occurred during the modelling period (March 2014 - November 2016).

	<b>Discharge of Floods (m<sup>3</sup>/s)</b>
Mean	141,2
Median	80.5
SD	164.8
Minimum	20.1
Maximum	570

**Table S4.** Characteristics of the model mesh.

	<b>Mean area (m<sup>2</sup>)</b>	<b>Median area (m<sup>2</sup>)</b>	<b>Minimum area (m<sup>2</sup>)</b>	<b>Maximum area (m<sup>2</sup>)</b>	<b>SD area (m<sup>2</sup>)</b>
Mesh elements	49.1	5.1	0.5	1949.9	96.9
Modelling domain	1,698,055	-	-	-	-



**Table S5.** Statistical summary of the modelled values for time since last flood and flooding frequency.

Time since last flood	Min	Max	Median	SD	Mean	CV (%)
February	131	463	131	86.6	187.9	46
May	24	553	24	120.2	63.8	188
August	53	653	63	123.9	85.2	145
October	5	715	5	147.8	54.6	271
Flood frequency (per year)	0.5	18.0	8.9	5.8	10.2	0.6

**Table S6.** Statistical distributions of the main environmental variables.

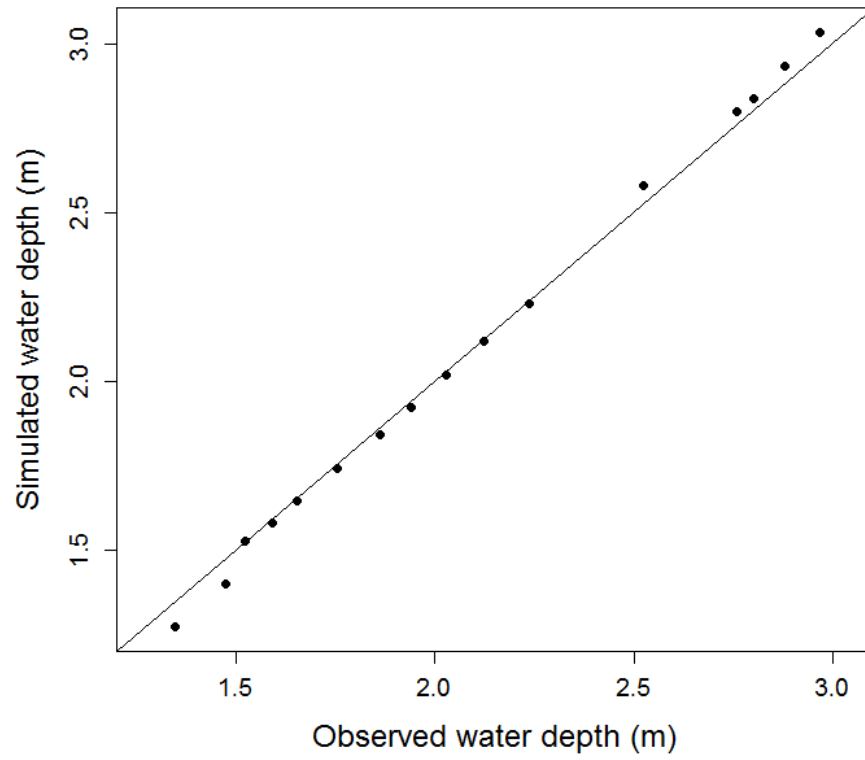
<b>Variable</b>	<b>Mean</b>	<b>Median</b>	<b>SD</b>	<b>Min</b>	<b>Max</b>
Conductivity ( $\mu\text{S}/\text{cm}$ )	72.8	73.1	14.9	36.1	101.0
pH	6.9	6.9	0.22	6.4	7.6
Nitrate ( $\text{mg}/\text{l}$ )	0.58	0.60	0.11	0.11	0.88
Dissolved Oxygen ( $\text{mg}/\text{l}$ )	9.1	9.1	1.5	4.5	11.8
Biofilm standing crop ( $\mu\text{g}/\text{l}$ )	7.7	6.6	4.4	0.9	22.3
Mean T ( $^{\circ}\text{C}$ )	10.8	10.2	3.9	2.2	19.2
SD T ( $^{\circ}\text{C}$ )	0.75	0.60	0.53	0	2.7
D <sub>50</sub> (cm)	6.0	7.0	2.9	0.1	14.3
Substrate diversity	1.3	1.4	0.4	0	1.7

**Table S7.** Contributions of the selected environmental variables to PCA axes 1 and 2.

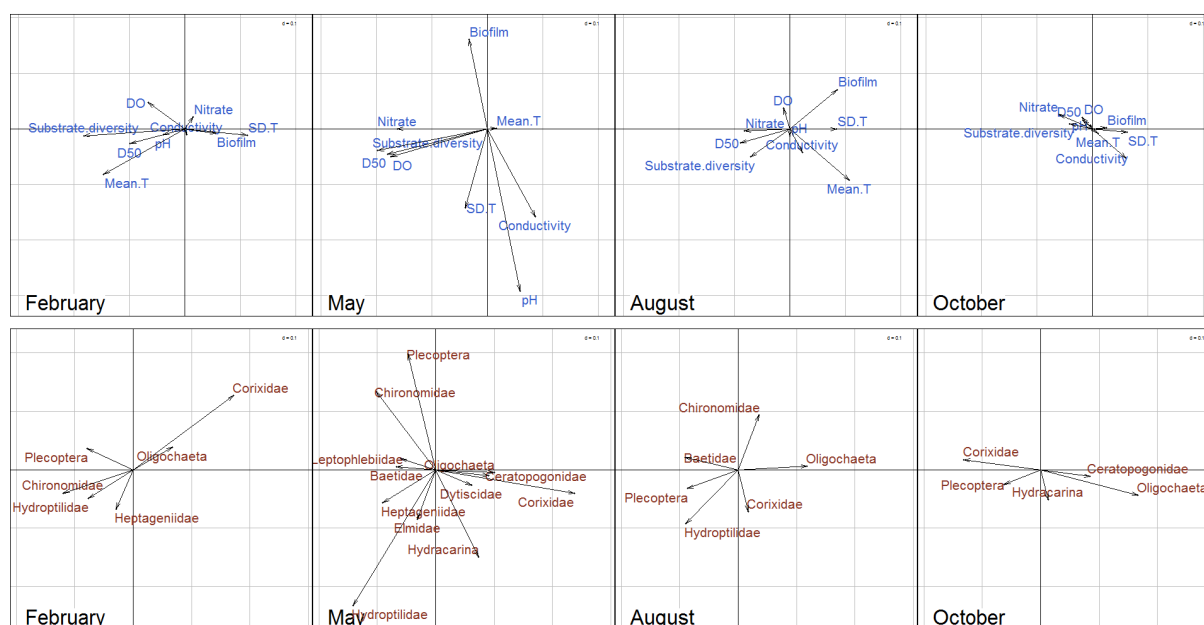
<b>Variable</b>	<b>PCA-1</b>	<b>PCA-2</b>
Conductivity	-0.416	-0.480
NO <sub>3</sub> -N	0.565	0.259
Dissolved Oxygen	0.491	-0.453
Mean T	-0.418	0.581
SD T	-0.300	-0.397

**Table S8.** Summary of the occurrence and density of sampled taxa.

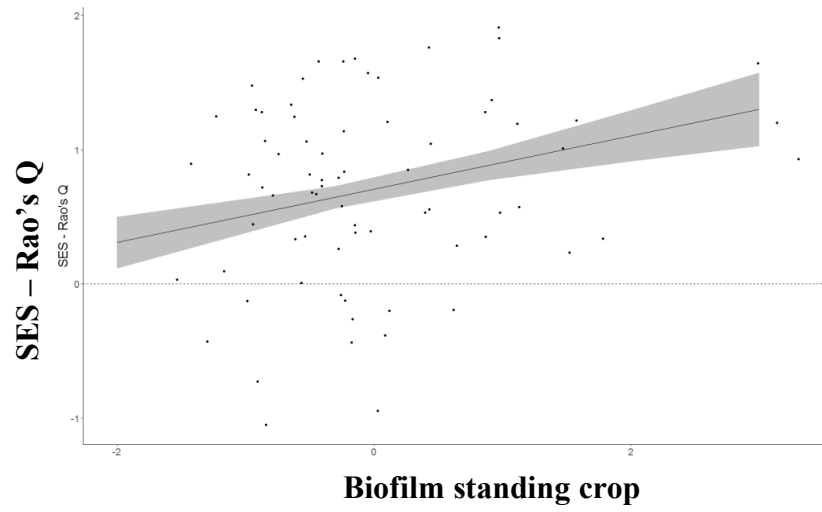
<b>Taxa</b>	<b>SD density</b>	<b>Min density</b>	<b>Max density</b>	<b>Mean density</b>	<b>Mean occurrence</b>
Oligochaeta	14.2	0	56.8	8.9	19.8
Hydracarina	7.0	0	27.3	6.2	21.0
Baetidae	38.1	0.25	178.0	14.9	20.8
Ephemerellidae	1.6	0	7.2	0.6	3.0
Heptageniidae	9.3	0	35.3	5.9	15.8
Leptophlebiidae	2.2	0	9.0	1.5	12.3
Plecoptera	17.5	1	69.8	18.5	23.3
Corixidae	97.0	0.25	458.0	46.8	20.3
Dytiscidae	3.9	0	16.3	2.6	12.3
Elmidae	2.9	0	13.5	1.2	8.5
Haliplidae	0.9	0	3.0	0.7	3.5
Hydroptilidae	40.9	0	169.0	23.2	19.0
Polycentropodidae	2.3	0	10.5	1.1	8.2
Ceratopogonidae	12.2	0	57.0	5.9	15.8
Chironomidae	165.0	7.5	708.0	133.0	23.3
Empididae	1.7	0	8.0	0.8	7.8
Limoniidae/Pediciidae	3.2	0	11.3	2.8	18.0
Tipulidae	7.3	0	32.8	5.5	15.5



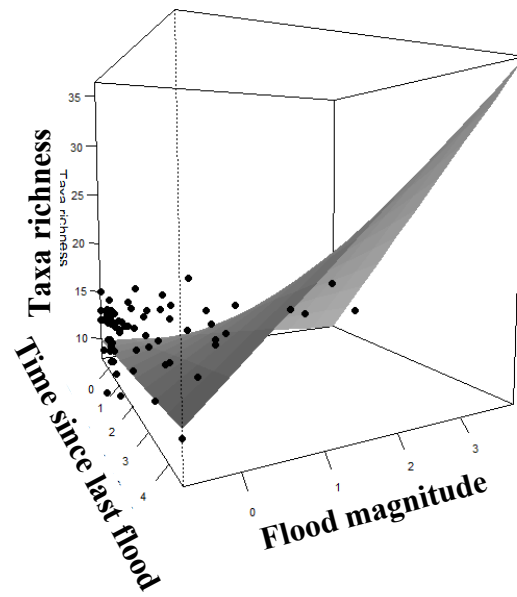
**Figure S1.** Plot showing the modelled versus observed water depth at the gauging station for  $k_{str} = 26$  and for a range of discharges.



**Figure S2.** Results of the STATICO analysis plotted separately for each sampling campaign. For clarity, species with projections values  $<0.05$  on both axes of the factorial plan were not displayed.



**Figure S3.** Relationship between SES Rao's Q and biofilm standing crop (scaled values).



**Figure S4.** Plot showing the interactive effect of time since last flood and flood magnitude (modelled bottom shear stress, scaled values) on taxa richness.



## Chapter 2

# Temporal variation in processes influencing community assembly among differentially connected habitat patches

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**Short title:** Metacommunity dynamics in floodplains

**Abstract:** Metacommunity theory provides a mechanistic approach towards understanding how spatial dynamics and local interactions shape community structure and biodiversity. In this respect, assembly processes in fluvial systems may fundamentally differ from many terrestrial systems due to hydrological connectivity (HC) and a highly dynamic physical environment. The spatial configuration of habitat patches and degree of connectivity to the regional species pool can be important determinants of dispersal and colonization in riverscapes. We created 24 ponds in a braided-river floodplain resulting in habitat patches with differing levels of hydrological and landscape connectivity (i.e., distance to source habitats of potential colonists). We measured ecosystem properties and aquatic macroinvertebrates over 45 days to assess the relative strength of processes contributing to community composition and functional diversity. We found that ponds with greater hydrological connectivity to the main stem had lower biofilm standing crops than those with reduced connectivity. Environmental differences among ponds resulted in metacommunities being structured by a combination of mass effects and species sorting during early stages of community assembly. Over time, the effect of the local environment diminished and trajectories in community structure converged, being strongly affected by landscape connectivity. Overall, the spatial location of ponds exerted a strong influence on community composition and functional diversity. This influence increasingly interacted with basal resource availability in the ponds over time. Our findings suggest that whilst the local environment constrains community assembly, its interaction with the spatial configuration of habitat patches can lead to different assembly trajectories through time.

**Key words:** metacommunity, stream invertebrates, connectivity, dispersal, community ecology, floodplain

## Introduction

Understanding the mechanisms underpinning patterns of species distributions, abundances and interactions is fundamental to community ecology (Logue et al. 2011). The term 'metacommunity' refers to local communities linked by the dispersal of multiple, potentially interacting species, where both local interactions and regional processes influence community assembly (Leibold et al. 2004, Holyoak et al. 2005). Bridging local processes and spatial patterns has been the focus of ecological research developing metacommunity theory in a wide range of ecosystems (Leibold et al. 2004, Holyoak et al. 2005).

Despite the four non-exclusive perspectives described in the classic metacommunity framework (Neutral Theory, Patch Dynamic, Species sorting, and Mass effects; see Hubbell 2001, Hanski 1994, Leibold 1995 and Holyoak 2005, respectively), all metacommunities are structured by a combination of two fundamental mechanisms: species sorting and dispersal (Lindström and Lagenheder 2012). Species sorting designates the filtering of species within a habitat patch by local abiotic conditions and biotic interactions, and results in clear species-environment linkages, provided dispersal is high enough to enable species to track variation in environmental conditions (Leibold 1995, Leibold et al. 2004, Soininen 2014). Dispersal rate (the flux of individuals between habitats) depends on the dispersal abilities of species in respect to the degree of connectivity between patches (Heino et al. 2015, Tonkin et al. 2016, Datry et al. 2016b). Mass effects can occur where excessively high dispersal rates give rise to source-sink dynamics that override environmental constraints, thus disrupting species-environment relationships (Leibold et al. 2004, Holyoak et al. 2005).

Reflecting these two fundamental mechanisms within the classic metacommunity framework, Cottenie (2005) suggested that most communities are located along a continuum between Species Sorting and Mass Effects, of which the position can vary in space and time (Holyoak et al. 2005, Datry et al. 2016a, Sarremejane et al. 2017). In this context, studies examining metacommunity dynamics should focus on the relative roles of dispersal and species sorting in community assembly (Winegardner et al. 2012).

The central role of connectivity in shaping metacommunities through dispersal is well established (Heino et al. 2015). Yet in freshwaters, hydrological connectivity (HC) can affect the composition of fish (Tockner et al. 1998, Fernandes et al. 2009), macroinvertebrate (Arscott et al. 2005, Paillex et al. 2007, Gaillard et al. 2008, 2014) and plankton communities (Gorski et al. 2013) by facilitating dispersal or by influencing local environmental conditions and thus the environmental filter (Paillex et al. 2009, 2013, Gaillard 2014). There is a general consensus that increasing spatiotemporal variation in HC results in increased biodiversity in floodplains (Ward et al. 1998, Amoros and Bornette 2002, Paillex et al. 2009), yet uncertainties remain regarding the relative importance of local HC-driven environment filtering and dispersal on metacommunity dynamics (Tonkin et al. 2016).

In floodplain systems, physico-chemical conditions within habitats diverge overtime (reflecting their level of HC and their position within the geomorphological setting), effectively creating a time-varying environmental filter for communities (Thomaz et al. 2007, Chang et al. 2016, Cadotte et al. 2017). In the initial phase of colonisation, strong aerial dispersers can colonize habitat patches in priority and track favourable environmental conditions (Leibold et al. 2004, Cadotte 2007, Soininen 2014), as local habitat conditions diverge, local environments select for species adapted to different environments (Chang et al. 2016). Finally, competitive

interactions may gain importance over time as a structuring force on communities (Fairchild et al. 2000, Mouquet et al. 2003, Cadotte 2007), and more so in resource-limited environments (Passy et al. 2017). The analysis of species functional traits related to dispersal ability and niche breadth may be particularly useful in identifying the relative importance of specific processes such as dispersal and environmental filtering in structuring communities (Thompson and Townsend 2006, Smith et al. 2015, Tonkin et al. 2016).

Functional diversity (FD), commonly defined as “the value and range of the functional traits of the organisms in a given ecosystem” (Diaz and Cabido 2001, Tilman 2001), has often been used by community ecologists to infer community assembly rules. This approach is based on the assumption that communities structured by the environment have low functional diversity because only adapted phenotypes are selected by the environmental filter (van der Valk et al. 1981, Keddy 1992, Diaz et al. 1999). In contrast, communities structured by strong interspecific competitive interactions have high functional diversity as a result of niche partitioning, a limiting similarity process (MacArthur and Levins 1967, Cornwell et al. 2009). Although patterns of FD must be interpreted with caution, their use within a temporal framework of community assembly can still provide robust evidence for different community assembly mechanisms (Li et al. 2015, Cadotte et al. 2017, Passy et al. 2017). Because FD reflects the balance between environmental filtering and competitive interactions within communities, it may increase overtime as a result of increasing competition (Fairchild et al. 2000, Mouquet et al. 2003, Cadotte 2007) but remain relatively low in environmentally harsher environments (Passy et al. 2017).

Here, we experimentally tested how the spatial configuration of habitat patches, and the degree of hydrological and landscape connectivity, influenced pond ecosystem properties and macroinvertebrate community assembly in a braided-river floodplain. We created 24 experimental ponds in a natural alluvial floodplain ecosystem and examined assembly dynamics of aquatic macroinvertebrates spanning seven weeks of sampling. The ponds were distributed within the active floodplain (i.e., the area around a stream regularly flooded on a periodic basis) to maximize differences in HC. Because the ponds are filled by exfiltration of hyporheic (i.e., shallow subterranean) water previously infiltrated from the river, we anticipated that pond location on the gravel bar would condition the length of hydrological flow paths and thus their degree of HC to the main river channel, thereby affecting physico-chemical properties (Boulton et al. 2008, Lowell et al. 2009, Larned and Datry 2013) and potential colonization through the hyporheos (Wood et al. 2010, van der Vorste et al. 2016). We further anticipated that different degrees of landscape connectivity (i.e., distance from source populations affecting dispersal and colonization; see below) would result from the respective location of each pond within the floodplain landscape.

We tested the following hypotheses: H1: Initial pond community composition would be structured by local environmental conditions resulting from differences in HC. H2: At later stages of community assembly, different levels of HC would lead to increasingly different environmental conditions within ponds (in terms of physico-chemistry and primary production) and this would be reflected in increasingly different community compositions. Following the initial colonization phase, individuals of some species might develop and emerge, thus enabling mass effects through aerial dispersal to dominate assembly processes. As a corollary, spatial structuring in community composition also could result from the mass effects mechanism. H3: Functional diversity (FD) would initially be low, reflecting the overall low taxonomic diversity, the different dispersal abilities of taxa and habitat selection by active dispersers. Over time, FD

would tend to increase as Species Sorting processes (i.e., niche differentiation) associated with strong interspecific competition develop. However, FD should remain lower within the least connected habitat patches, reflecting the environmental filtering in these harsher, more stressful environments.

## Methods

### *Study floodplain*

The Maggia River floodplain is located in the southern Swiss canton of Ticino and is characterized by a pluvio-nival hydrological regime (average annual discharge  $3.87 \text{ m}^3/\text{s}$ ) with a typical snowmelt flood-peak in June (Ruf, 2007). The dynamic flow regime and high bedload transport rate maintain a braided structure in the floodplain, with characteristic gravel bars and vegetated islands.

Twenty-four ponds (ca.  $3 \times 3 \text{ m}$  each) were excavated in two gravel bars of the floodplain using a mechanical digger (Figure 1). Twelve ponds (ponds 1-12) were located on a gravel bar that also contained a natural floodplain pond, whereas the other 12 ponds (ponds 13-24) were situated on a gravel bar further upstream. Both groups of ponds were separated from each other by the main channel of the river (ca. 8 m wetted width). On each gravel bar, 6 ponds were located at the downstream end (ponds 1-6 and 13-18, respectively) and 6 at the upstream end (ponds 7-12 and 19-24, respectively) to maximize differences in physico-chemistry related to the length of hyporheic flow paths.

Each pond was immediately filled with upwelling hyporheic water. All ponds were fed directly with upwelling subsurface waters, but pond 9 also became fed by substantial inflow of surface water from the main channel and was subsequently removed from analysis. Ponds were distributed in clusters where average, minimum, and maximum distances between ponds were 153, 3, and 322 m, respectively (Figure 1).



**Figure 1.** Experimental setup showing the approximate location of the natural and experimental ponds within the study floodplain.

### *Field sampling and sample processing*

Field sampling occurred on days 15, 20, 30 and 45 after the ponds were excavated. This period of 45 days is longer than the average return period of 33 days for flows above  $20 \text{ m}^3/\text{s}$  (between 2006 and 2016), which have been observed to inundate parafluvial habitats in the Maggia floodplain (data from the Swiss Federal Office for the Environment). On each visit, a water sample (0.5 L) was collected from the center of each pond and stored on ice in the dark

for chemical analysis in the laboratory. In the laboratory, water samples were analysed for calcium (Ca, mg/L), nitrate (NO<sub>3</sub>, mg/L), phosphorus (PO<sub>4</sub>, mg/L), and pH using standard methods following Tockner et al. (1997). Spot measurements of dissolved oxygen (mg/L, Hach HQ40d connected to a LD10101 oxygen probe), water temperature (°C), and electrical conductivity (µS/cm, WTW meter, Germany) were taken in the center of each pond. The order in which ponds were sampled was randomized at each sampling event to reduce bias of collection time.

Biofilm was measured by randomly selecting 5 stones (cobble-size) within each pond. Biofilm was removed from each rock by scrubbing with a wire brush into a plastic container with 100 mL of distilled water, and the scrubbed area measured (after Uehlinger 1991). The biofilm suspension was subsequently filtered through a glass fiber filter (0.45 µm, Whatman GFF) and stored on ice in the dark. Chlorophyll-a extraction was conducted by incubating each filter in 6 mL 90% ethanol at 70°C for 10 minutes. Chlorophyll-a (µg /L) was then determined using standard spectrophotometry (Hitachi 2000) following methods in Meyns et al. (1994).

Macroinvertebrates were sampled in each pond on each date using a kick-net (250 µm mesh). A standard surface area (~ 90 cm<sup>2</sup>) was disturbed for 30 seconds and the net was pulled 10 times through the suspended material. A different section of each pond was sampled on each sampling event to minimize disturbance effects. This method was suitable for collecting invertebrates as substrate size and benthic primary production in each pond section appeared relatively homogeneous. Macroinvertebrate samples were subsampled to one quarter and all individuals counted and identified to the lowest possible taxonomic level using Tachet et al. (2010).

### *Data analysis*

To evaluate our predictions, we first examined initial colonization patterns in relation to differences in ecosystem properties (i.e., physico-chemical characteristics and basal resource availability), HC and spatial location among ponds (H<sub>1</sub>). We then assessed temporal shifts in community assembly in relation to the spatial gradient in environmental conditions and HC among ponds (H<sub>2</sub>). Lastly, we evaluated functional diversity measures to infer community assembly rules in relation to spatially-structured environmental factors (H<sub>3</sub>). All statistical tests were completed at the level of significance  $\alpha = 0.05$ .

*Hydrological connectivity* - We performed a principal component analysis (PCA) for each sampling date to examine physico-chemical differences in the ponds that reflected the length of hyporheic flow paths (i.e., HC). The PCAs used six abiotic variables: electrical conductivity, pH, nitrate, phosphorus, water temperature and dissolved oxygen. We also measured the distance between each pond and the assumed location of upstream surface-water infiltration (corresponding to the upstream tip of the gravel bar). This distance metric was previously used by Larned and Datry (2013) and proved to be a robust proxy for the length of hyporheic flow paths. PCA1 explained 42.5%, 31.7%, 37.2% and 58.3% of the total variation at days 15, 20, 30 and 45, respectively. As the distance to the upstream infiltration zone was strongly correlated to PCA1 for each sampling date (Appendix S1: Table S2), this distance metric (in m) was used as the main environmental determinant of HC. We also examined the effect of the distance to the upstream infiltration zone on water electrical conductivity and on chlorophyll-a (as a measure of standing primary production) with a linear mixed effect model (GLMM) using sampling date as a random effect to correct for temporal autocorrelation.

*Community composition* – Because community composition was affected by the influence of a few highly abundant taxa, macroinvertebrate abundances were Hellinger-transformed to increase the resolution for changes in community structure. We first conducted a NMDS analysis at each date to explore the differences in community composition among ponds and dates. We then used partial redundancy analysis to partition the variance in community structure between HC, environmental variables (electrical conductivity, dissolved oxygen, nitrate and phosphorus concentrations, water temperature and chlorophyll a) and the spatial positioning of the ponds (Y coordinate) at each date. For this, we first conducted a forward selection procedure at each date, and used the full set of retained variables as “environmental drivers” at all 4 dates. The forward selection was completed using 999 permutations of residuals under a reduced model with stopping criteria at a significance level of  $\alpha = 0.05$  and an adjusted  $R^2$  equal to that of the global model with all environmental variables included. This was performed with the function `ordiR2step` of the `vegan` package (Oksanen et al. 2017) in R (R core team, 2017). Because the X and Y coordinates of the ponds were highly correlated (Pearson’s coefficient = 0.98), the spatial component consisted of the Y coordinate, which increased in the upstream direction.

In order to investigate the temporal changes in the effects of HC, environmental conditions and spatial positioning of the sites on community composition, we used the multivariate STATICO method (Simier et al. 1999, Thioulouse et al. 2004), which is well adapted to studying the temporal variability of species-environment relationships (Simier et al. 2006, Carassou and Ponton 2007, Mendes et al. 2012, Marques et al. 2011). Data was organized into a succession of coupled tables of environmental descriptors and species abundances, each pair of tables corresponding to a sampling date. The STATICO method is a combination of the co-inertia analysis (Doledec and Chessel, 1994) and the Partial Triadic Analysis (Thioulouse and Chessel 1987). It proceeds in three stages: the first stage analyses each table one-by-one with PCA; the second stage consists in linking each pair of tables (a pair for each date) by co-inertia to find axes that maximize the covariance between row coordinates of species and environment matrices; finally, a partial triadic analysis is used to analyze the sequence of cross-covariance tables and produces a compromise, or mean species-environment co-structure for all dates. STATICO allows the graphical representation of the projection of sites (in the original species and environmental tables) on the compromise axes, and thus a straightforward analysis of temporal change in species-environment linkages. The analysis and plotting were conducted in R with the `ade4` package (Thioulouse et al. 1997).

*Dispersal-related traits* - We used four dispersal-related trait classes obtained from the Tachet database (Tachet et al. 2010) and used in previous studies (Tonkin et al. 2016). This database provides an affinity of a given taxa for a particular trait class using a fuzzy coding approach ranging from 0 for low affinity to 3 for high affinity. The four classes were “aquatic passive dispersal”, “aquatic active dispersal”, “aerial passive dispersal” and “aerial active dispersal”. For each trait class, we calculated a community-level weighted mean (CWM), which is the mean trait value of all species present in the community, weighted by their relative abundances. We used the `dbFD` function from the `FD` package in R (Laliberté and Legendre, 2010). We used a generalized linear mixed model (GLMM) to examine relationships between the four CWMs, the gradient of HC, and the spatial location of the ponds (Y coordinate) over time. Sampling day also was included as a random effect to correct for temporal autocorrelation.



Functional diversity metrics - Functional diversity (FD) was calculated as the standardized effect size of Rao's quadratic entropy (SES-RaoQ), calculated as the standard deviation of the observed RaoQ from that of a null model. The null model was constructed by shuffling species abundances within each site and calculating RaoQ at each of 999 iterations. This type of null model approach, commonly used in functional diversity studies, has the advantage of removing the influence of differences in species richness on FD (Mason et al. 2013). For the analysis, we used all biological traits available in our database and used in previous studies on floodplain systems (e.g., Paillex et al. 2013, Van der Vorste et al. 2016), amounting to 41 categories distributed in 9 biological traits (Appendix S1: Table S3). Functional traits for all taxa were obtained from the Tachet database for each taxon (Tachet et al. 2010). In order to give the same weight to all traits in the diversity measure, affinity scores were standardized so that their sum for a given taxon would equal 1 (see Paillex et al. 2013). We used a generalized linear mixed model (GLMM) to examine the relationship between FD, the gradient of hydrological conductivity and the spatial location of the ponds (Y coordinate) over time. An interactive term between fixed effects was added and sampling date was also used as a random effect to control for temporal autocorrelation.

## Results

### *Hydrological connectivity*

The distance to the upstream tip of the gravel bar was strongly associated with PCA1 and positively related to electrical conductivity (Appendix S1: Figure S1). The strong association between electrical conductivity and the distance to the infiltration zone ( $p < 0.001$ ,  $R^2_{adj} = 0.84$ , estimate =  $-0.5 \pm 0.06$ , Appendix S1: Figure S2) indicates that this distance metric is a robust proxy for the length of hyporheic flow paths (i.e., hydrological connectivity). For clarity, we used the opposite of the distance to infiltration zone as gradient of HC in this study;  $HC = -1 * (\text{distance to infiltration zone})$ . We refer to the further downstream ponds as "less connected" in the rest of this study as these received older water with higher electrical conductivity, whereas the more upstream ponds are referred to as "more connected" as they primarily received younger water derived from the surface flow of the river. Chlorophyll-a, as a proxy for standing primary production, increased over time, from  $25.8 \pm 22.7 \mu\text{g/L}$  (Day 15) to  $177.3 \pm 85.0 \mu\text{g/L}$  (Day 45) (mean  $\pm 1$  SD; Appendix S1: Figure S3, Table S4), and was negatively correlated to HC ( $p = 0.002$ ,  $R^2_{adj} = 0.59$ , estimate =  $-0.91 \pm 0.27$ ).

### *Macroinvertebrate colonization patterns*

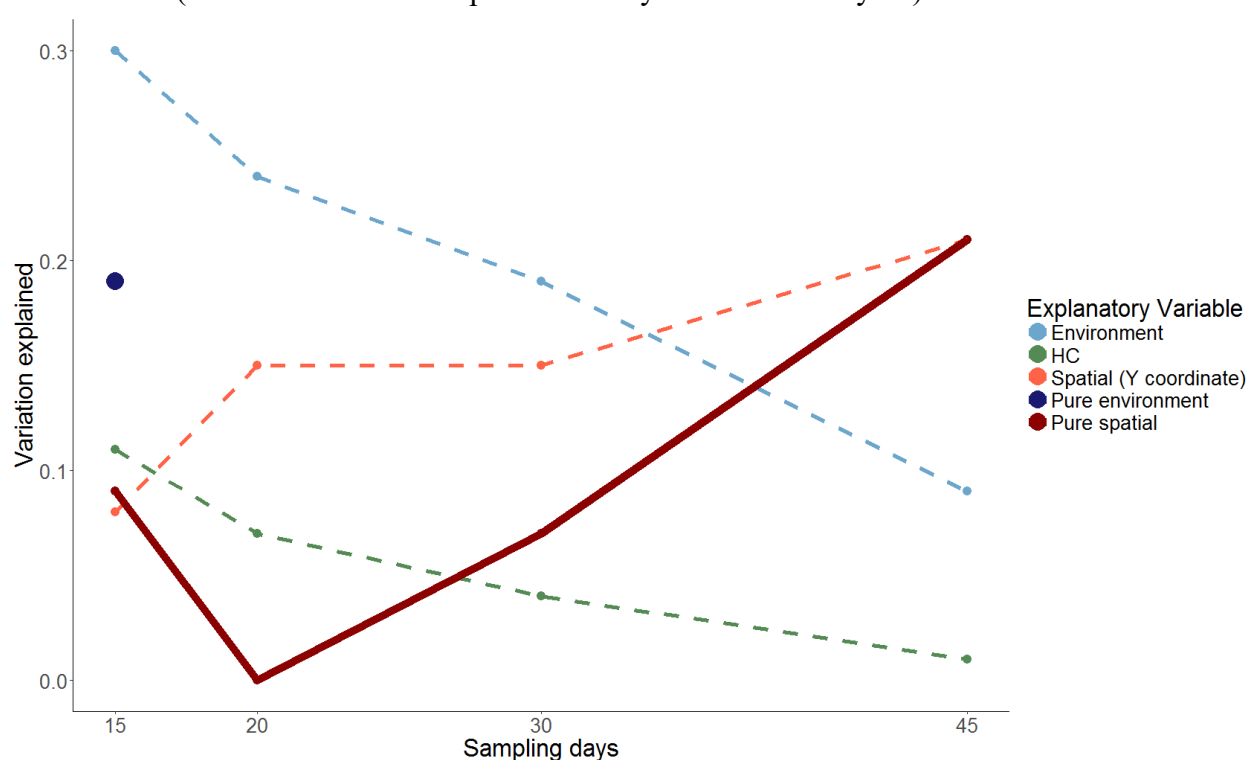
Total taxa richness was relatively constant through time, whereas mean taxa richness, mean community evenness and mean Shannon diversity slightly decreased from Day 15 to Day 30 and increased at Day 45. Both the mean and total invertebrate densities increased over time (Appendix S1, Table S5). At Days 15 and 20, macroinvertebrate densities were negatively correlated to HC ( $p$  value = 0.006, estimate =  $-3.14 \pm 1.02$  at Day 15, and  $p$  value = 0.006, estimate =  $-2.82 \pm 0.9$  at Day 20).

From the NMDS plots, it appears that differences in HC were largely reflected in community composition at Day 15. The sensitive and predominantly rheophilic taxa were more abundant in well-connected sites and the more lentic taxa in less connected sites (Appendix S1, Figure S4). Similar patterns were observed at Day 20. At Day 30, no cluster of sites in terms of

community composition was clearly identifiable, except ponds 13, 15, 16, 17 and 18 (the sites with low HC on the upstream gravel bar), which had more specific community structures. Finally, at Day 45, community composition among ponds appeared to be ordered in a downstream-upstream direction, suggesting that some spatial structuring may be occurring.

*Relative effects of hydrological connectivity, environmental variables and spatial structure on macroinvertebrate community assembly*

The variance partitioning analysis showed that overall, the relative effects of HC and environmental drivers decreased over time, whereas the influence of the spatial location of ponds increased (Figure 2; see Appendix S1, Table S6 and Figure S5 for detailed results). When considering shared effects with other variables, both HC and environmental drivers had significant effects, decreasing from Day 15 to Day 30 (from 11% to 1% and from 30% to 9% variance explained between Day 15 and 45, respectively). However, only the pure effect of environmental variables was significant at Day 15 (19% variance explained). Finally, the pure effect of the spatial location of ponds increased sharply at Day 45 (from 9% variance explained at Day 15 to 21% at Day 45), whereas its shared effect with the environmental variables decreased over time (from 19% variance explained at Day 15 to 8% at Day 45).



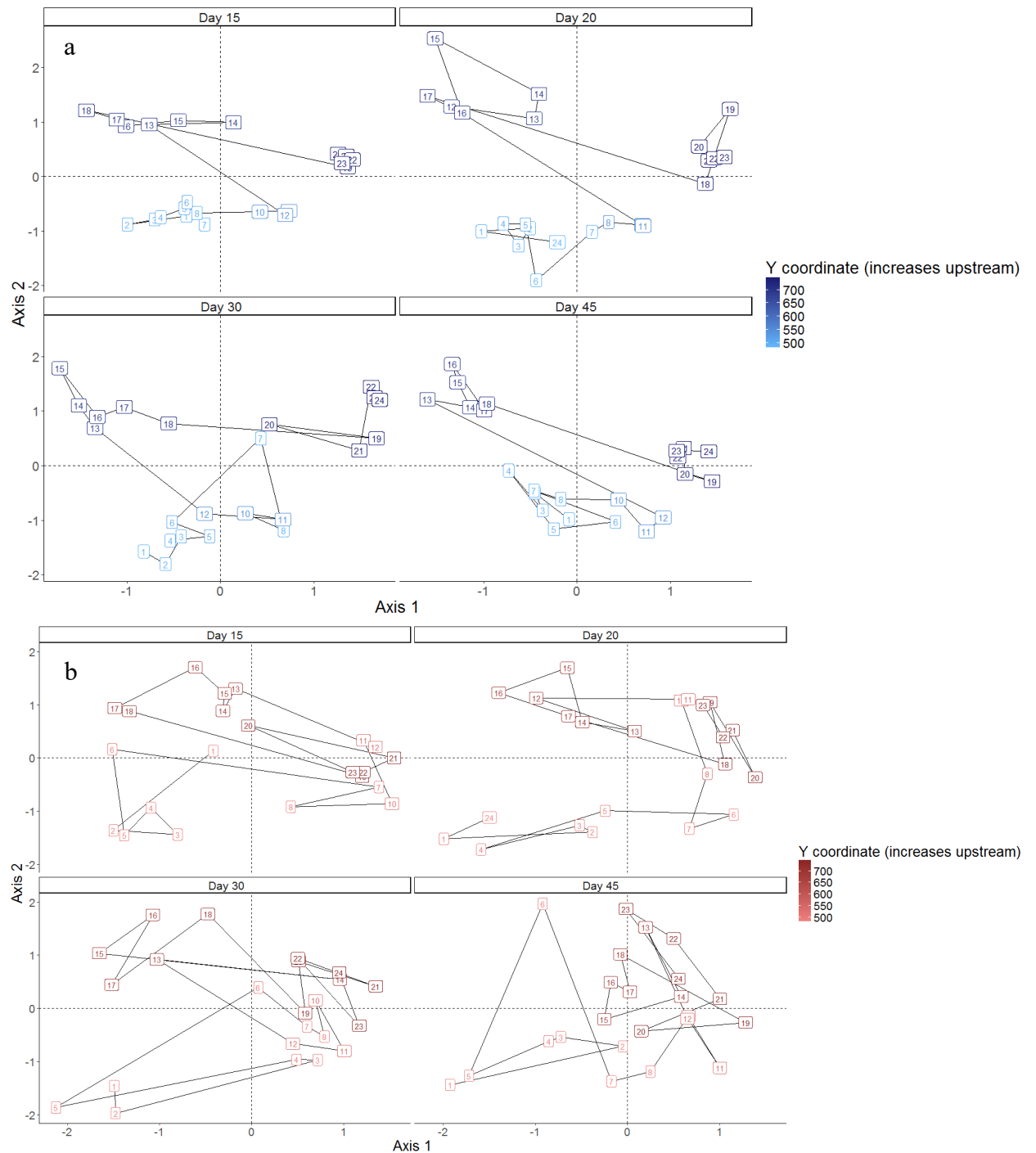
**Figure 2.** Plot showing the amount of variation in community composition explained at each date by hydrological connectivity (HC), environmental descriptors (electrical conductivity, dissolved oxygen, nitrate and phosphorus concentrations, and chlorophyll a) and the spatial location of the ponds along the Y coordinate. Both the confounded effects (effect of a variable interacting with the two others, dashed lines) and pure effects (effect of a variable corrected for the other two, solid lines) are displayed. The pure environmental effect only figures as one point at Day 15 because it was non-significant at all other dates.

*Temporal variation in species-environment relationships.*

*Inter-structure* - The STATICO analysis showed that statistically significant co-structure between environmental descriptors and community composition occurred at all sampling dates (p values = 0.001, 0.001, 0.001 and 0.009 at Days 15, 20, 30 and 45), and explained 55.4% of the variation with two axes (34.5% and 20.9% of variance explained by axes 1 and 2, respectively). The analysis of the inter-structure revealed that the fourth sampling date contributed the least to the compromise (contributions to the first eigenvalue of the compromise = 0.81, 0.82, 0.80 and 0.55 for Days 15, 20, 30 and 45, respectively), meaning that the co-structure between the pair of environmental descriptors and species distribution tables was weaker at this date.

*Compromise* - Axes 1 and 2 of the compromise were clearly dominant in terms of explanatory power, accounting for 55.8% and 33.8% of the total explained variance, respectively. Axis 1 was primarily structured by the opposition between sites with high HC and high DO levels on the positive side (contributions = 0.28 and 0.33, respectively) and sites with low HC, high electrical conductivity (contribution = -0.31) and high chlorophyll a (contribution = -0.17) on the negative side. Axis 2 was largely structured by the spatial location of sites along the Y coordinate (contribution = 0.35), and the upstream sites (greater Y) also had slightly higher chlorophyll a and lower nitrate concentrations (contributions = 0.19 and -0.15, respectively; Appendix S1: Table S7, Figure S6a).

The co-structure between environmental descriptors and species abundances was composed of two components: the local hydrological connectivity and associated environmental gradient, and the spatial location of the ponds. The analysis of species scores on the compromise suggested that these two components often interacted to constrain community composition. For instance, the predominantly lentic taxa Culicinae and Hydrophilidae both favoured habitats with low HC but Culicinae were predominantly found at downstream sites (low Y coordinate), whereas Hydrophilidae were more abundant at upstream sites. The two rheophilic taxa Baetidae and Nemouridae mainly occurred at the well-connected and oxygenated sites. Finally, Tanytarisni, Orthocladiinae and Chironomini were mainly found at the well-connected and oxygenated sites located upstream (high Y coordinate), whereas Oligochaetes were found in similar environments but predominantly downstream (Appendix S1: Table S8, Figure S6b).



**Figure 3.** Projections of the site scores in terms of environmental descriptors (a) and species abundances (b) on the compromise axes at each date.

*Trajectories* - The projection of environmental descriptors and species at each date on the first two axes of the compromise allowed for the visualization of the temporal variability in the biota-environment relationship. At Day 15, local conditions within sites were clearly segregated along axis 1 and this had a clear effect on community composition with the mainly rheophilic taxa Heptageniidae, Baetidae, Ephemerella and Oligochaete being more abundant at well-connected sites and the mainly lentic taxa Culicinae and Hydrophilidae at sites with low HC (Appendix S1: Figure S7 a, b). Axis 2 accounted for the spatial location of sites as well as

their level of HC. This interaction between HC and the spatial component affected the distribution of Hydrophilidae and Orthoclaadiinae, which favoured sites with low HC and were more abundant upstream. At Days 20 and 30, the first axis of the compromise still represented the gradient of HC, but the second axis then accounted for the interaction between the spatial location of the sites and their level of chlorophyll a as well as their phosphorus and nitrate concentrations. Species distributions were then constrained by the interaction between space and environment, with no clear separation between rheophilic and lentic taxa (Appendix S1: Figure S7 c, d, e and f). At Day 45, the effect of environmental descriptors had decreased to a minimum and only the spatial location of the ponds remained as the single variable affecting community composition, mostly through high abundances of Tanytarisni upstream (Appendix S1: Figure S7 g, h).

The analysis of the sites scores for environmental descriptors (Figure 3a) suggested that environmental differences among sites remained relatively constant through time, with clear spatial clustering (site groups 1 to 6 and 13 to 18 were characterized by low HC and located respectively downstream and upstream, and other sites being well-connected), although conditions on the lower gravel bar appeared to slightly converge at Day 45. In contrast, the projection of sites scores for species abundances showed that community composition mirrored the environmental variability at day 15, but converged over time until Day 45 where the co-structure was no longer identifiable and sites were instead organized along axis 2, representing the spatial location of the ponds (Figure 3 b).

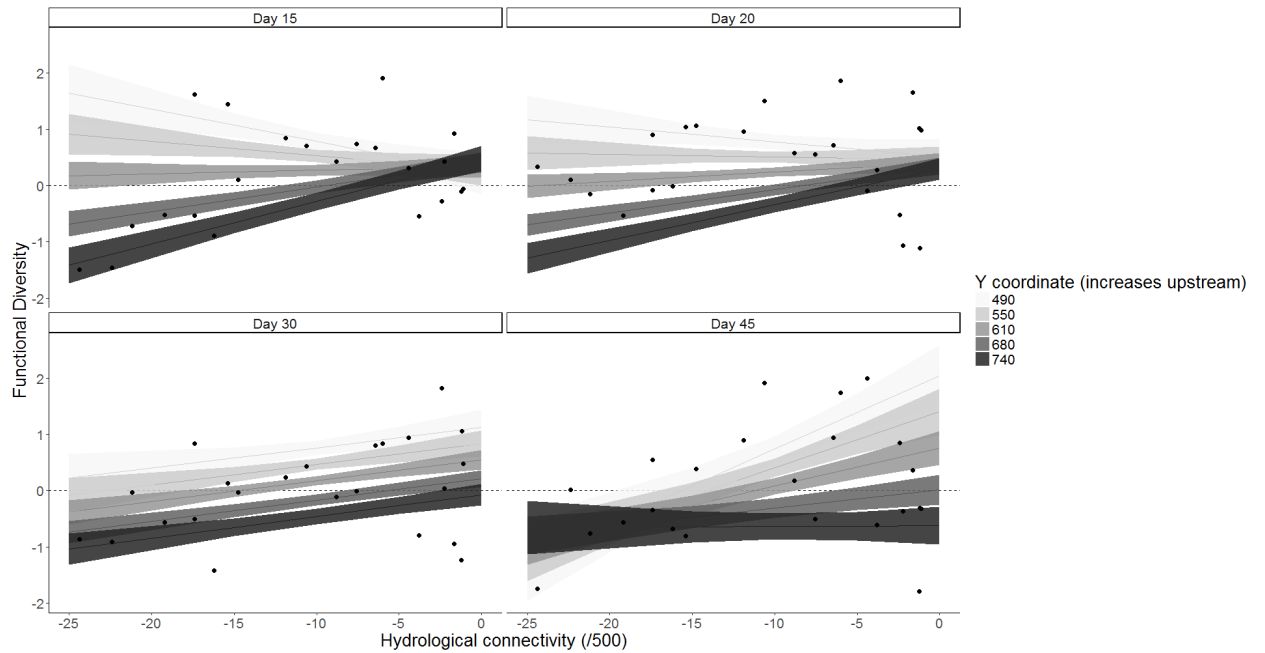
#### *Effects of hydrological and landscape connectivity on dispersal-related traits*

The CWM for the trait “aquatic passive dispersal” was positively related to the level of HC ( $p = 0.03$ , estimate =  $1.03 \pm 0.45$ , appendix S1, Table S9). The CWM for the trait “aerial passive dispersal” was negatively correlated to the gradient of HC ( $p = 0.025$ , estimate =  $-1.07 \pm 0.45$ ,) and positively correlated to the Y coordinate of the ponds (Y increases in the upstream direction,  $p = 0.003$ , estimate =  $1.05 \pm 0.32$ ) and to time (in days,  $p = 0.003$ , estimate =  $0.08 \pm 0.01$ ). The CWM for the trait “aerial active dispersal” was negatively correlated to the Y coordinate of the ponds ( $p = 0.01$ , estimate =  $-1.45 \pm 0.37$ ). The CWM for the trait “aquatic active dispersal” was not affected by any of the hydrological or spatial metrics.

#### *Effects of hydrological and landscape connectivity on functional diversity*

Functional diversity was significantly and negatively correlated to the level of HC ( $p = 0.004$ , estimate =  $-61.85 \pm 20.76$ , Appendix S1: Table S10; Figure 4). FD also increased over time ( $p = 0.007$ , estimate =  $0.239 \pm 0.084$ ). Time had significant positive interactions with HC ( $p = 0.006$ , estimate =  $2.145 \pm 0.736$ ) and a negative one with the Y coordinate ( $p = 0.006$ , estimate =  $-0.363 \pm 0.124$ ). FD was positively affected by the interaction between HC and the Y coordinate ( $p = 0.002$ , estimate =  $97.16 \pm 30.69$ ). The three way interaction between sampling day, HC and the Y coordinate also had a negative effect on functional diversity ( $p = 0.006$ , estimate =  $-3.169 \pm 1.087$ ). At Day 15, FD of well-connected ponds was centered around the zero line and did not vary with the Y coordinate. In contrast, FD of less connected ponds varied greatly with the Y coordinate. Specifically, ponds located downstream (lower Y coordinate) were functionally over-dispersed with regard to the null expectation and ponds located upstream were functionally clustered with respect to the null expectation. For ponds located upstream (High Y coordinate), an increasing pattern of FD with increasing HC was noticeable at all dates. However, for

downstream ponds, the pattern of decreasing FD with increasing HC was present only at Days 15 and 20, whereas an opposite pattern emerged at dates 30 and 45, where FD increased with increasing HC.



**Figure 4.** Relationship between functional diversity (FD) and hydrological connectivity (measured as:  $-1 \times \text{distance to infiltration zone (m)}$ ) at Days 15, 20, 30 and 45. The different regression lines represent the effect of HC on FD at various distances from the floodplain pond (m) modelled as a continuous explanatory variable.

## Discussion

Classical metacommunity theory implies that community assembly in a habitat patch is determined jointly by local properties and regional processes such as dispersal (Leibold et al. 2004). Further, temporal variation in processes contributing to community assembly can be particularly important in highly dynamic ecosystems (Fukami and Nakajima 2011, Datry et al. 2016a) such as alluvial floodplains, where habitat patches (e.g., floodplain ponds) undergo frequent cycles of disturbance and recovery (Tockner and Stanford 2002). In riverine ecosystems, assembly processes may fundamentally differ from many terrestrial landscapes due to hydrological connectivity and a highly dynamic physical environment (Palmer et al. 2000). Here, we tested how the degree of hydrological connectivity and spatial configuration of habitat patches affected community assembly in an alluvial floodplain over time. We used a novel field experiment that simulated the creation of floodplain ponds and monitored macroinvertebrate community assembly over 45 days. We found that the interaction between the local environment (here, the level of HC) and the spatial configuration of habitat patches (the probable degree of connectivity to the regional species pool) influenced community structure and shifts in assembly rules, leading to different assembly trajectories through time.

### *Direct and indirect influence of hydrological connectivity on community composition*

At early stages of community assembly, our results showed that communities were organized along gradients of measured environmental variables (being largely dependent on the degree of HC) and to some extent along the Y-axis spatial coordinates of the sites, partially supporting H1. We found that pond location with regard to longitudinal hyporheic flow-paths was an important driver of HC, as reflected in physico-chemical differences among ponds along this gradient. Changes in major ion concentrations and dissolved oxygen along hyporheic flow paths are well-documented in alluvial floodplain systems (Malard et al. 1999, Boulton et al. 2008, Lowell et al. 2009, Larned and Datry 2013). These findings are consistent with previous work showing that the geomorphic setting of habitat patches (here, floodplain ponds) often determines abiotic characteristics of patches and respective biota in natural floodplains (Amoros and Bornette 2002, Brunke et al. 2003, Opperman et al. 2010). Importantly, we further showed from analysis of dispersal-related traits that HC directly affected macroinvertebrate communities by enabling aquatic passive dispersers to colonize the ponds via hyporheic flow paths. Several benthic macroinvertebrates are known to use the hyporheic zone for dispersal (Wood et al. 2010, Van der Vorste et al. 2016). In addition, the lower abundance of aerial passive dispersers at sites with high HC suggests that colonization through the hyporheos at these sites may have prevented aerial dispersers from establishing. It is well established that depending on immigration timing, a given species can encounter very different probabilities of colonization success in new habitats (Fukami & Nakajima 2011). The stochastic nature of such “priority effects”, more broadly defined as the sequence of species immigration, determines the effect of biotic interactions on community structure (Schoener 1976, Drake 1991, Almany 2003).

### *Proximity to late-successional habitat can cause mass effects under low HC*

A novel finding of our study was that the interplay between the spatial location of patches and HC induced temporal shifts in metacommunity structure and assembly rules. A shift occurred from communities being initially constrained by a combination of environmental and spatial variables to a predominantly spatial structuring later in assembly, partially supporting H2. This contrasts with the general view that species sorting is a primary structuring force in lentic freshwater communities (Cottenie 2005, Vanschoenwinkel et al. 2007, Waterkeyn et al. 2008). The species-environment relationships at Day 15 highlighted in the STATICO trajectory analyses suggested that individuals could track differences in environmental variation (resulting from different levels of HC) and preferentially colonize favorable habitats. Concomitantly, the spatial location of the ponds had a slight constraining effect on community composition. During later community development, environmental filtering effects diminished while the spatial structuring component remained high. Vanschoenwinkel et al. (2010) reported a similar shift from local species sorting to mass effects in a temporary pool metacommunity, induced by late colonization of aerial dispersers. At Day 45, while community composition in ponds at the lower gravel bar (near the natural floodplain pond) differed from those at the upper gravel bar, they remained more segregated in relation to local environmental differences. In contrast, pond communities at the upstream gravel bar converged in composition, dominated by a particular pool of species (e.g., Tanytarsini).

A very likely explanation for the influence of the spatial location of ponds is that the colonization of individual ponds was influenced by dispersal of individuals from an existing large natural floodplain pond at the downstream end of the study area. This effectively would

equate the Y coordinate to a measure of the spatial distance between each habitat and this natural pond, which increases with Y. Preferential colonization on the downstream gravel bar may only have occurred at less connected ponds with relatively high primary production as suggested by their separate community composition. Whereas ponds with low HC and primary production had similar community composition irrespective of spatial location.

This finding is further supported at Day 15 by the FD values in the less connected ponds: FD was positive in the ponds of the downstream gravel bar (in the vicinity of the floodplain pond), indicating that some process of limiting similarity may be acting, and negative upstream, suggesting that environmental filtering processes occurred there. Although FD patterns must be interpreted with care (Cadotte et al. 2017, Kraft et al. 2015), they are nevertheless useful in drawing inferences on assembly rules, especially when analyzed over time (Li et al. 2015). FD increased over time, suggesting an overall increase in limiting similarity, but it remained lower at sites located further upstream at Days 30 and 45, only partially supporting H3. This indicated that a downstream location (in the vicinity of the natural floodplain pond) favoured the development of interspecific competitive interactions. In general, communities in older habitats tend to be dominated by competitive interactions (Fairchild et al. 2000, Mouquet et al. 2003, Cadotte 2007) and mass effects from aerial dispersal are known to occur in the vicinity of large sources of colonists in lentic invertebrate communities (Vanschoenwinkel et al. 2007). Considering the increasing influence of the spatial location of the ponds within the landscape and therefore potentially of the distance to the natural floodplain pond (a highly productive habitat at a later stage of succession) and the higher relative abundance of aerial active dispersers in its vicinity, it is likely that it directly influenced assembly rules in nearby ponds by dispersal, thereby sustaining high FD. On the other hand, experimental ponds distantly located from the natural pond likely were exposed to colonization by a particular pool of species that generally perform better in these environments (e.g., Tanytarsini), potentially outcompeting other species. Louette et al. (2008) reported such priority effects in a similar experimental system.

Because our sampling specifically targeted aquatic-stages of macroinvertebrates, the delay in the importance of landscape connectivity could be due to life histories of aerial-active dispersers. For example, it has been proposed that generation time can change the balance between species sorting and mass effects (Mouquet and Loreau 2003), with species with shorter generation times favouring local species sorting (Cottenie et al. 2003). Given that the duration of the experiment was 45 days, the trajectories in later community composition among ponds remain unknown. However, we evaluated community assembly for a period of time greater than the return period of ca. 33 days for floods above 20 m<sup>3</sup>/s (average 2006-2016) in this system, flows known to effect parafluvial habitats in the floodplain. Thus, whilst we cannot conclude whether assemblages had reached a stable state at Day 45, communities in natural ponds are likely to be often reset to earlier phases of assembly before reaching that stage.

Our findings imply that species sorting by local environmental conditions is the primary structuring process in the early phase of community assembly, and that the emergence of mass effects over time is influenced by the spatial location of the habitat within the landscape, especially with regard to potential sources of colonists. A major finding contributing to a further understanding of metacommunity dynamics was that the interplay between environmental conditions and proximity to late successional habitats during community assembly can influence the balance between species sorting and mass effects over time. Knowledge on the effects of connectivity and dispersal on metacommunity structure has profound implications for the



management of fragmented landscapes, especially regarding disturbance regimes (Staddon et al. 2010). In practice, our findings suggest that restoring high spatial heterogeneity in hydrological disturbance and connectivity is essential for maintaining biodiversity in alluvial floodplains, which may act as 'spatial insurance' for ecosystem functioning and stability in heterogeneous floodplain landscapes (Loreau et al. 2003). Specifically, resource managers should aim at protecting and restoring hydrological connectivity between habitats by including different flow regimes to maintain heterogeneity in successional stages of floodplain habitats.

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## References:

- Almany, G.R. 2003. Priority effects in coral reef fish communities. *Ecology* 84: 1920–1935.
- Amoros, C., and Bornette, G. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology* 47: 761-776.
- Arscott, D. B., Tockner, K., and Ward, J. V. 2005. Lateral organization of aquatic invertebrates along the corridor of a braided floodplain river. *J. N. Amer. Benthol. Soc* 24: 934-954.
- Borcard, D., & Legendre, P. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling* 153: 51-68.
- Borcard, D., Legendre, P., Avois-Jacquet, C., and Tuomisto, H. 2004. Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85: 1826-1832.
- Boulton, A. J., Datry, T., Kasahara, M., and Stanford, J. A. 2008. Ecology and management of the hyporheic zone: stream–groundwater interactions of running waters and their floodplains. *Freshwater Science* 29: 26-40
- Brunke, M., Hoehn, E., and Gonser, T. 2003. Patchiness of River–Groundwater Interactions within Two Floodplain Landscapes and Diversity of Aquatic Invertebrate Communities. *Ecosystems* 6: 707-722.
- Cadotte, M. W. 2007. Competition-colonization tradeoffs and disturbance effects at multiple scales. *Ecology* 88:823- 829.
- Cadotte, M. W., and Tucker, C. M. 2017. Should Environmental filtering be abandoned? *Trends in Ecology and Evolution* 32: 429-437.
- Carassou, L., and Ponton, D. 2007. Spatio-temporal structure of pelagic larval and juvenile fish assemblages in coastal areas of New Caledonia, southwest Pacific. *Marine Biology* 150: 697-711.
- Chang, C., and HilleRisLambers, J. 2016. Integrating succession and community assembly perspectives. *F1000Research*, 5, F1000 Faculty Rev–2294.
- Cornwell, W.K., & Ackerly, D.D. 2009. Community assembly and shifts in the distribution of functional trait values across an environmental gradient in coastal California. *Ecological Monographs* 79: 109–126.
- Cottenie, K., Michels, E., Nuytten, N., and De Meester, L. 2003. Zooplankton metacommunity structure: regional vs. Local processes in highly interconnected ponds. *Ecology* 84:991-1000.
- Cottenie, K. 2005. Integrating environment and spatial processes in ecological community dynamics. *Ecology Letters* 8:1175-1182.
- Datry, T., Bonada, N., and Heino, J. 2016a. Towards understanding the organization of metacommunities in highly dynamic ecological systems. *Oikos* 125: 149-159.
- Datry, T., Pella, H., Leigh, C, Bonada, N. and Hugueny, B. 2016b. A landscape approach to advance intermittent river ecology. *Freshwater Biology* 61: 1200-1213
- Diaz, S., Cabido, M. and Casanoves, F. 1999. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* 9: 113–122.
- Diaz, S., and Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in ecology and Evolution* 11: 646-655.
- Dolédec, S. and Chessel, D. 1994. Co-inertia analysis: an alternative method for studying species–environment relationships. *Freshwater Biology*. 31: 277-294

- Drake, J.A. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. *American Naturalist* 137: 1-26.
- Erős, T., Sály, P., Takács, P., Specziár, A., and Bíró, P. 2012. Temporal variability in the spatial and environmental determinants of functional metacommunity organization - stream fish in a human-modified landscape. *Freshwater Biology* 57: 1914-1928.
- Erős, T., Sály, P., Takács, P., Higgins, C. L., Bíró, P., and Schmera, D. 2013. Quantifying temporal variability in the metacommunity structure of stream fishes: the influence of non-native species and environmental drivers. *Hydrobiologia* 722: 31-43.
- Fairchild, G. W., Faulds, A. M., and Matta, J. F. 2000. Beetle assemblages in ponds: effects of habitat and site age. *Freshwater Biology* 44: 523-534.
- Fernandes, R., Gomes, L. C., Pelicice, F. M., and Agostinho, A. A. 2009. Temporal organization of fish assemblages in floodplain lagoons: the role of hydrological connectivity. *Environ Biol Fish* 85: 99-108.
- Fukami, T., & Nakajima, M. 2011. Community assembly: alternative stable states or alternative transient states? *Ecology Letters* 14: 973-984.
- Gallardo, B., Garcia, M., Cabezas, A., Gonzalez, E., Gonzalez, M., Ciancarelli, C., and Comin, F. A. 2008. Macroinvertebrate patterns along environmental gradients and hydrological connectivity within a regulated river-floodplain. *Aquatic Sciences* 70: 248-258
- Gallardo, B., Doledéc, S., Paillex, A., Arscott, D. B., Sgeldon, F., Zilli, F., Mérigoux, S., Castella, E., and Comin, F. A. 2014. Response of benthic macroinvertebrates to gradients in hydrological connectivity: a comparison of temperate, subtropical, Mediterranean and semiarid river floodplains. *Freshwater Biology* 59: 630-648.
- Gorski, K., Collier, K. J., Duggan, I. C., Taylor, C. M., and Hamilton, D. P. 2013. Connectivity and complexity of floodplain habitats govern zooplankton dynamics in a large temperate river system. *Freshwater Biology* 58: 1458-1470.
- Hanski, I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* 63: 151-162.
- Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton, NJ: Princeton University Press.
- Heino, J., Melo, A. S., Siquiera, T., Soininen, J., Valanko, S., and Bini, L. M. 2015. Metacommunity organisation, spatial extent, and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology* 60: 845-869.
- Holyoak, M., Leibold, M. A., Mouquet, N. M., Holt, R. D., and Hoopes, M. F. 2005. Metacommunities - A framework for large-scale community ecology. - *Metacommunities: Spatial Dynamics and Ecological Communities*: 1-31.
- Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of vegetation science* 3: 157-164
- Kraft, N. J. B., Godoy, O., and Levine, J. M. 2015 Plant functional traits and the multidimensional nature of species coexistence. *PNAS* 112: 797-802.
- Laliberté, E., and P. Legendre 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299-305
- Larned, S. T., and Datry, T. 2013. Flow variability and longitudinal patterns in parafluvial water chemistry, aquatic invertebrates and microbial activity. *Freshwater Biology* 58: 2126-2143.

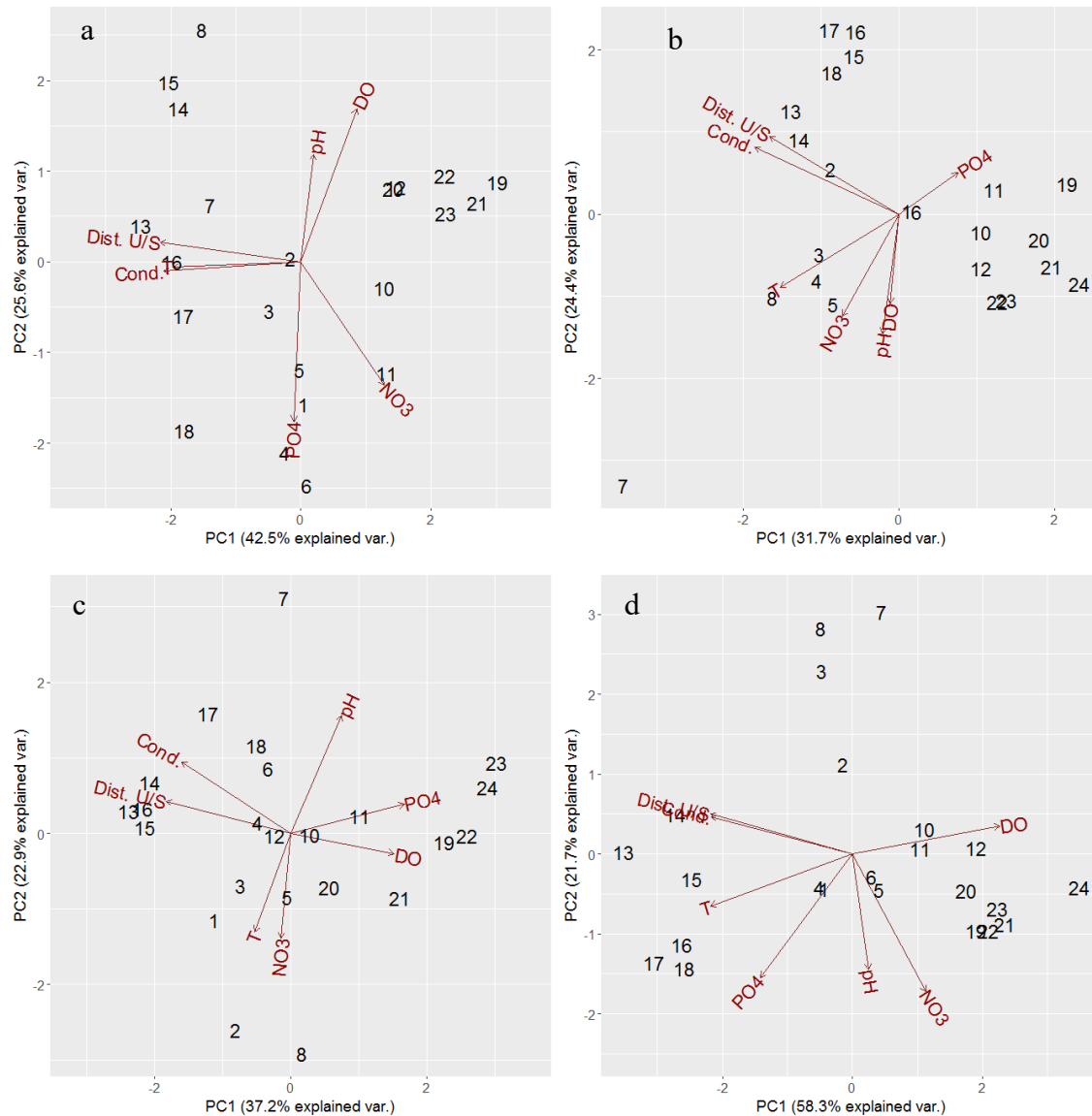
- Leibold, M. A. 1995. The niche concept revisited: Mechanistic models and community context. *Ecology* 76: 1371–1382.
- Leibold, M., A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J., B., Law, R., Tilman, D., Loreau, M., and Gonzalez, A. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7: 601-613
- Lowell, J. L., Gordon, N., Engstrom, D., Stanford, J. A., Holben, W. E., and Gannon, J. E. 2009. Habitat heterogeneity and associated microbial community structure in a small-scale floodplain hyporheic flow path. *Microbial Ecology* 58: 611-620.
- Li, S., Cadotte, M. W., Meiners, S. J., Hua, Z., Jiang, L., and Shu., W. 2015. Species colonisation, not competitive exclusion, drives community overdispersion over long-term succession. *Ecology Letters* 18: 964-973.
- Lindström, E. S., and Lagenheder, S. 2012. Local and regional factors influencing bacterial community assembly. *Environmental Microbiology Reports*, 4:1-9.
- Logue, J. B., Mouquet, N., Peter, H., and Hillebrand, H. 2011. Empirical approaches to metacommunities: A review and comparison with theory. *Trends in Ecology & Evolution* 26: 482-491.
- Loreau, M., Mouquet, N., and Gonzalez, A. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. *PNAS* 100: 12765-12770.
- Louette, G., De Meester, L., and Decklerck, S. 2008. Assembly of zooplankton communities in newly created ponds. *Freshwater Biology* 53: 2309-2320.
- MacArthur, R.H. & Levins, R. 1967. Limiting similarity convergence and divergence of coexisting species. *American Naturalist* 101: 377–385.
- Malard, F., Tockner, K. and Ward J. V. 1999. Shifting dominance of subcatchment water sources and flow paths in a glacial floodplain, Val Roseg, Switzerland. *Arctic, Antarctic, and Alpine Research* 31: 135-150.
- Marques, S. S., Pardal, M. A., Mendes, S, and Miranda Azeiteiro, U. 2011. Using multitable techniques for assessing the temporal variability of species–environment relationship in a copepod community from a temperate estuarine ecosystem. *Journal of experimental marine biology and ecology*. 405:59-67.
- Mason, N. W. H., de Belo, F., Mouillot, D., Pavoine, S., and Dray, S. 2013 A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science* 24: 794-806.
- McCluney, K. E., LeRoy Poff, N., Palmer, M. A., Thorp, J. H., Poole, G. C., Williams, B. S., Williams, M. R., and Baron, J. S. 2014. Riverine macrosystems ecology: sensitivity, resistance, and resilience of whole river basins with human alterations. *Frontiers in Ecology and the Environment* 12: 48-58.
- Mendes, S., Fernandez-Gomez, M. J., Jorge Pereira, M., Miranda Azeiteiro, U., and Purificación Galindo-Villardón, M., 2012. An empirical comparison of canonical correspondence analysis and STATICO in the identification of spatio-temporal ecological relationships. *Journal of Applied Statistics*. 39: 979-
- Meyns, S., R. Illi, and B. Ribi. 1994. Comparison of chlorophyll-a analysis by HPLC and spectrophotometry: Where do the differences come from? *Archiv für Hydrobiologie*, 132: 129–139.

- Mouquet, N., and Loreau, M. 2003. Community patterns in source-sink metacommunities. *American Naturalist* 162: 554-557.
- Mouquet, N., Munguia, P., Kneitel, J. M., and Miller, T. E. 2003. Community assembly time and the relationship between local and regional species richness. *Oikos* 103: 618-626.
- Oksanen, J., Blanchet, G., Friendly, M., Roeland, K., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, H. H., Szoecs, E., Wagner, H. 2017. *vegan: Community Ecology Package*. R package version 2.4-2.
- Opperman J. J., Luster, R., McKenney, B. A., Roberts, M., and Wrona Meadows, A. 2010. Ecologically functional floodplains: connectivity, flow regime and scale. *Journal of the American water resources association* 46: 211-226.
- Paillex, A., Castella, E., and Carron, G. 2007. Aquatic macroinvertebrate response along a gradient of lateral connectivity in river floodplain channels. *Journal North American Benthological Society* 26: 779-796.
- Paillex, A., Doledec, S., Castella, E., and M rigoux, S. 2009. Large river floodplain restoration: predicting species richness and trait responses to the restoration of hydrological connectivity. *Journal of Applied Ecology* 46: 250-258.
- Paillex, A., Doledec, S., Castelly, E., M rigoux, S., and Aldridge, D. C. 2013. Functional diversity in a large river floodplain: anticipating the response of native and alien macroinvertebrates to the restoration of hydrological connectivity. *Journal of applied ecology* 50: 97-106.
- Palmer, M, Swan, C. M., Nelson, K., Silver, P., and Alvestad, R. 2000. Streambed landscapes: evidence that stream invertebrates respond to the type and spatial arrangement of patches. *Landscape Ecology* 15: 563-576.
- Passy, S.I., Bottin, M., Soininen, J., and H. Hillebrand. 2017. Environmental filtering and taxonomic relatedness underlie the species richness–evenness relationship. *Hydrobiologia* 787: 243.
- R Core Team 2017. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Ruf, W. 2007. Numerical modelling of distributed river-aquifer coupling in an alpine floodplain. ETH Z rich. Doctoral Thesis. Diss. ETH No. 17534.
- Sarremejane R, Ca edo-Arg elles M, Prat N, Mykr  H, Muotka T, and Bonada N. 2017. Do metacommunities vary through time? Intermittent rivers as model systems. *Journal of Biogeography* 44: 2752–2763.
- Schoener, T.W. 1976. Alternatives to Lotka – Volterra competition: models of intermediate complexity. *Theoretical Population Biology* 10: 309–333.
- Simier, M., Blanc L., Pellegrin, F., and Nandris, D. 1999. Approche simultan e de K couples de tableaux: application   l tude des relations pathologie v g tale – environnement *Revue de statistique appliqu e*, 47 : 31-46.
- Simier, M., Laurent, C., Ecoutin, J-M., Albaret, J-J. 2006. The Gambia River estuary: a reference point for estuarine fish assemblage studies in West Africa *Estuarine, Coastal and Shelf Science*, 69: 615-628
- Smith, R. F., Venugopal, P. D., baker, M. E., and Lamp, W. O. 2015. Habitat filtering and adult dispersal determine the taxonomic composition of stream insects in an urbanizing landscape. *Freshwater Biology* 60:1740-1754

- Soininen, J. 2014. A quantitative analysis of species sorting accross organisms and ecosystems. *Ecology* 95: 3284-3292
- Staddon, P., Lindo, Z., Crittenden, P. D., Gilbert, F., and Gonzalez, A. 2010. Connectivity, non-random extinction and ecosystem function in experimental metacommunities. *Ecology Letters*, 13: 543-552
- Tachet H., Bournaud M., Richoux P., and Usseglio-Polatera P. 2010. Invertébrés d'eau douce - systématique, biologie, écologie. CNRS Editions, Paris. Accessed through [www.freshwaterecology.info](http://www.freshwaterecology.info) - the taxa and autecology database for freshwater organisms, version 7.0 accessed on 23.02.2018.
- Thioulouse, J. and Chessel, D. 1987. Les analyses multitableaux en écologie factorielle. I. De la typologie d'état à la typologie de fonctionnement par l'analyse triadique. *Acta Oecol.-Oec. Gen.* 8: 463-480.
- Thioulouse, J., Chessel, D., Dolédec, S., and Olivier, J.M. 1997. ADE-4: a multivariate analysis and graphical display software. *Statistics and Computing*, 7: 75-83.
- Thioulouse, J., Simier, M. and Chessel, D. 2004. Simultaneous analysis of a sequence of paired ecological tables. *Ecology*, 85: 272-283
- Thompson, R., and Townsend, C. 2006. A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. *Journal of Animal Ecology* 75: 476-484
- Tilman D. Functional diversity. 2001 In: Levin SA, editor. *Encyclopedia of Biodiversity*. Elsevier; Oxford: pp. 109–120.
- Tockner, K., Malard, F., Burgherr, P., Robinson, C. T., Uehlinger, U., Zah, R., Ward, J. V. 1997. Physico-chemical characterization of channel types in a glacial floodplain ecosystem (Val Roseg, Switzerland). *Archiv für Hydrobiologie* 140: 433–463.
- Tockner, K., Schiemer F. and Ward J.V. 1998. Conservation by restoration: the management concept for a river floodplain system on the Danube River in Austria. *Aquatic Conservation* 8: 71–86.
- Tockner, K. and Stanford, J. A. 2002. Riverine flood plains: present state and future trends. *Environmental Conservation* 29: 308–330.
- Tonkin, J., Stoll, S., Jähnig, S., and Hase, P. 2016. Contrasting metacommunity structure and beta diversity in an aquatic-floodplain system. *Oikos* 125: 686-697.
- Uehlinger, U. 1991. Spatial temporal variability of the periphyton biomass in a prealpine river (Necker, Switzerland). *Archiv für Hydrobiologie* 123: 219–237.
- Van der Valk, A.G. 1981. Succession in wetlands: a Gleasonian approach. *Ecology* 62: 688–696.
- Van der Vorste, R., Malard, F., and Datry, T. 2016. Is drift the primary process promoting the resilience of river invertebrate communities? A manipulative field experiment in an intermittent alluvial river. *Freshwater Biology* 61: 1276-1292.
- Vanschoenwinkel, B., De Vries, C., Seaman, M., and Brendonck, L. 2007. The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient. *Oikos* 116:1255-1266
- Vanschoenwinkel, B., Waterkeyn, A., Jocqué, M., Boven, L., Seaman, M., and Brendonck, L. 2010. Species sorting in space and time – the impact of disturbance regime on community

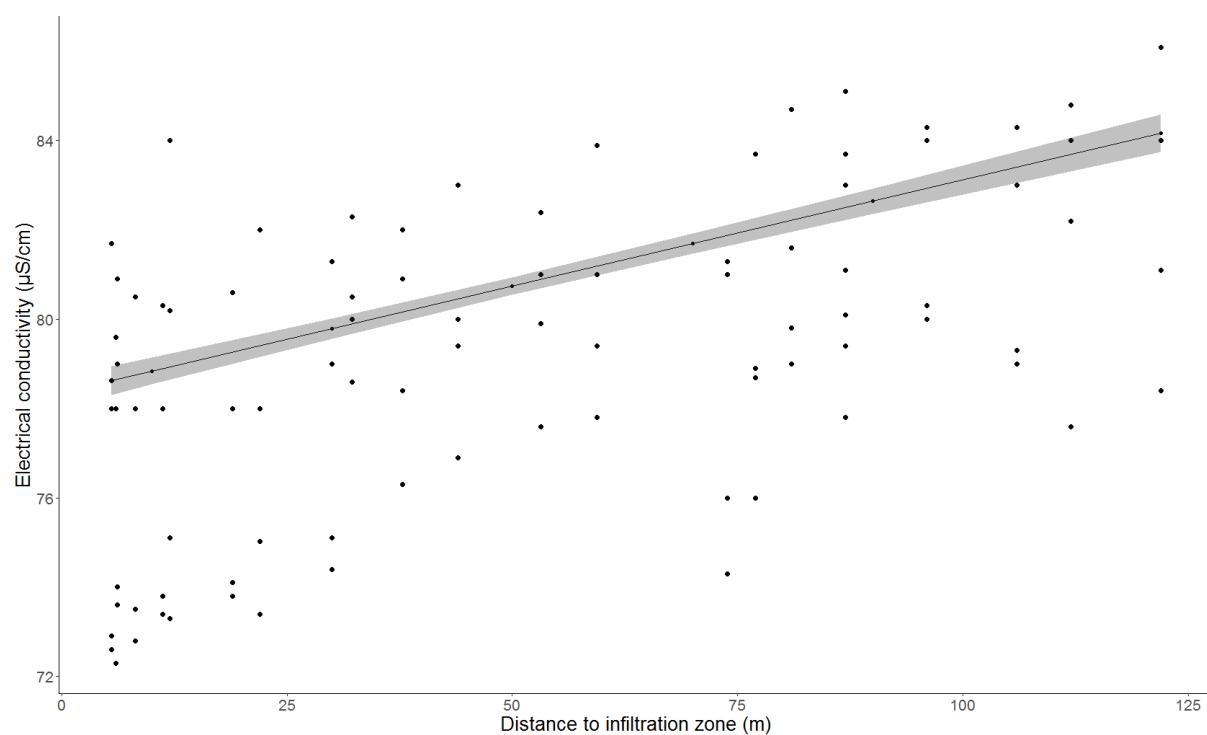
- assembly in a temporary pool metacommunity. *Journal North American Benthological Society* 29: 1267-1278.
- Ward, J. V. 1998. Riverine landscapes: Biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation* 83: 269-278.
- Ward, J. V., Tockner, K., Arscott, D. B., and Claret, C. 2002. Riverine landscape diversity. *Freshwater Biology* 47: 517-539.
- Waterkeyn, A., Grillas, P., Vanschoenwinkel, B., and Brendonck, L. 2008. Invertebrate community patterns in Mediterranean temporary wetlands along hydroperiod and salinity gradients. *Freshwater Biology* 53: 1808-1822.
- Winegardner, A. K., Jones, B. K., Ng, Y. S. Y., Siqueira, T., and Cotneie, K. 2012. The terminology of metacommunity ecology. *Trends in Ecology and Evolution* 73:253-254.
- Wood, P. J., Boulton, A. J., Little, S., and Stubbington, R. 2010. Is the hyporheic zone a refugium for aquatic macroinvertebrates during severe low flow conditions? *Fundamental and Applied Limnology* 176: 377-390.

## Supporting Information

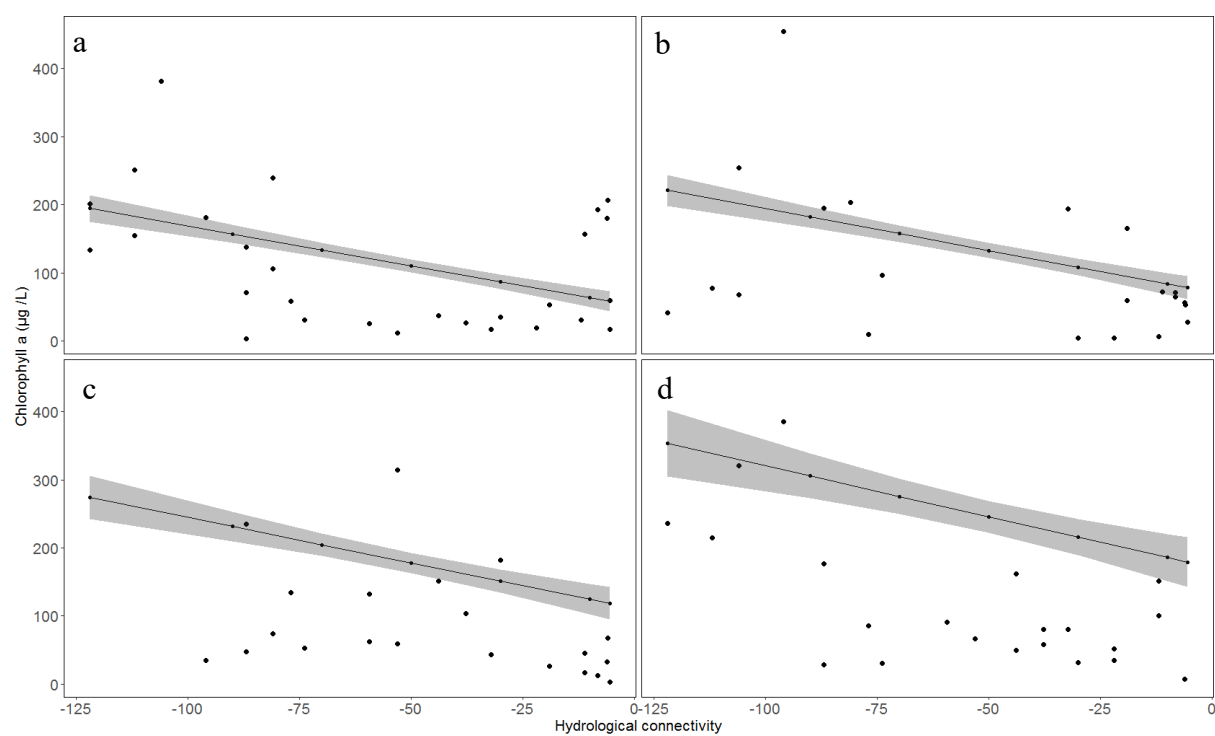


**Figure S1.** Principal component analysis on the distance between a pond and the upstream end of the gravel bar (Dist. U/S), electrical conductivity (Cond.,  $\mu\text{S}/\text{cm}$ ), pH, nitrate concentration ( $\text{NO}_3$ ,  $\text{mg}/\text{L}$ ), phosphorus concentration ( $\text{PO}_4$ ,  $\text{mg}/\text{L}$ ), water temperature ( $T$ ,  $^{\circ}\text{C}$ ) and dissolved oxygen ( $\text{DO}$ ,  $\text{mg}/\text{L}$ ) at Days 15 (a), 20 (b), 30 (c) and 45 (d). Numbers represent individual pond numbers.

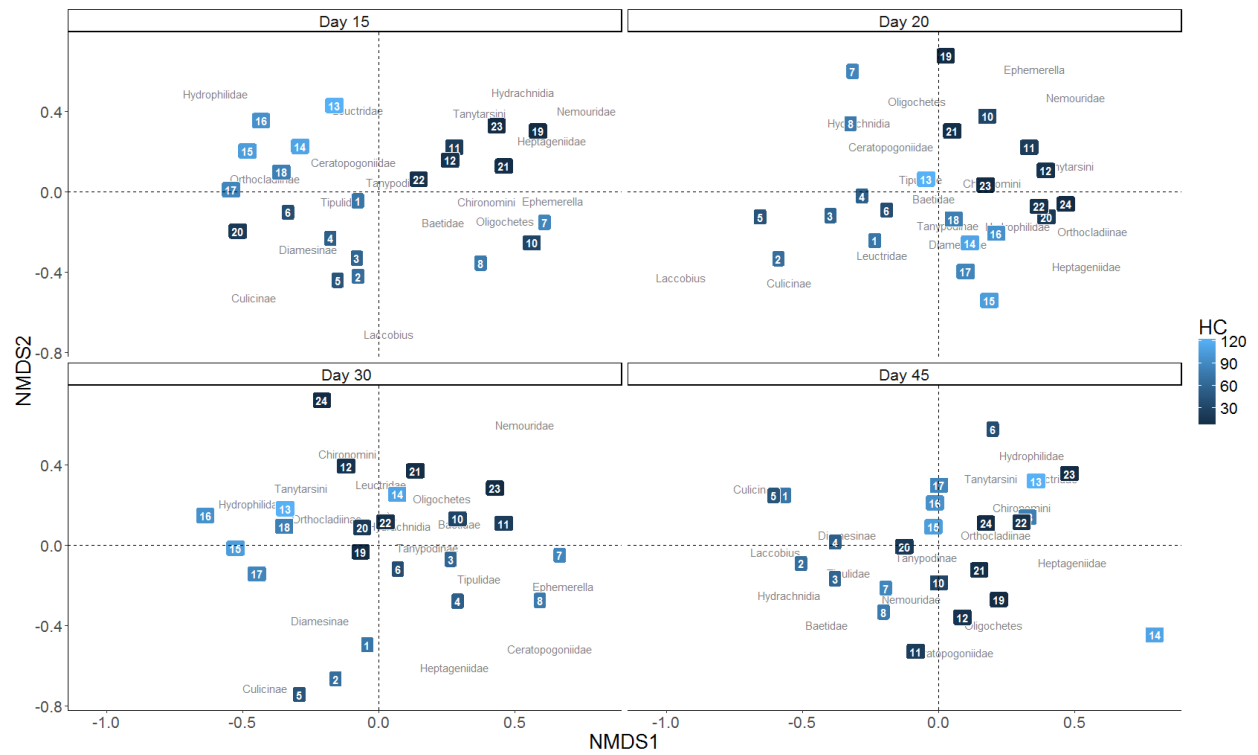




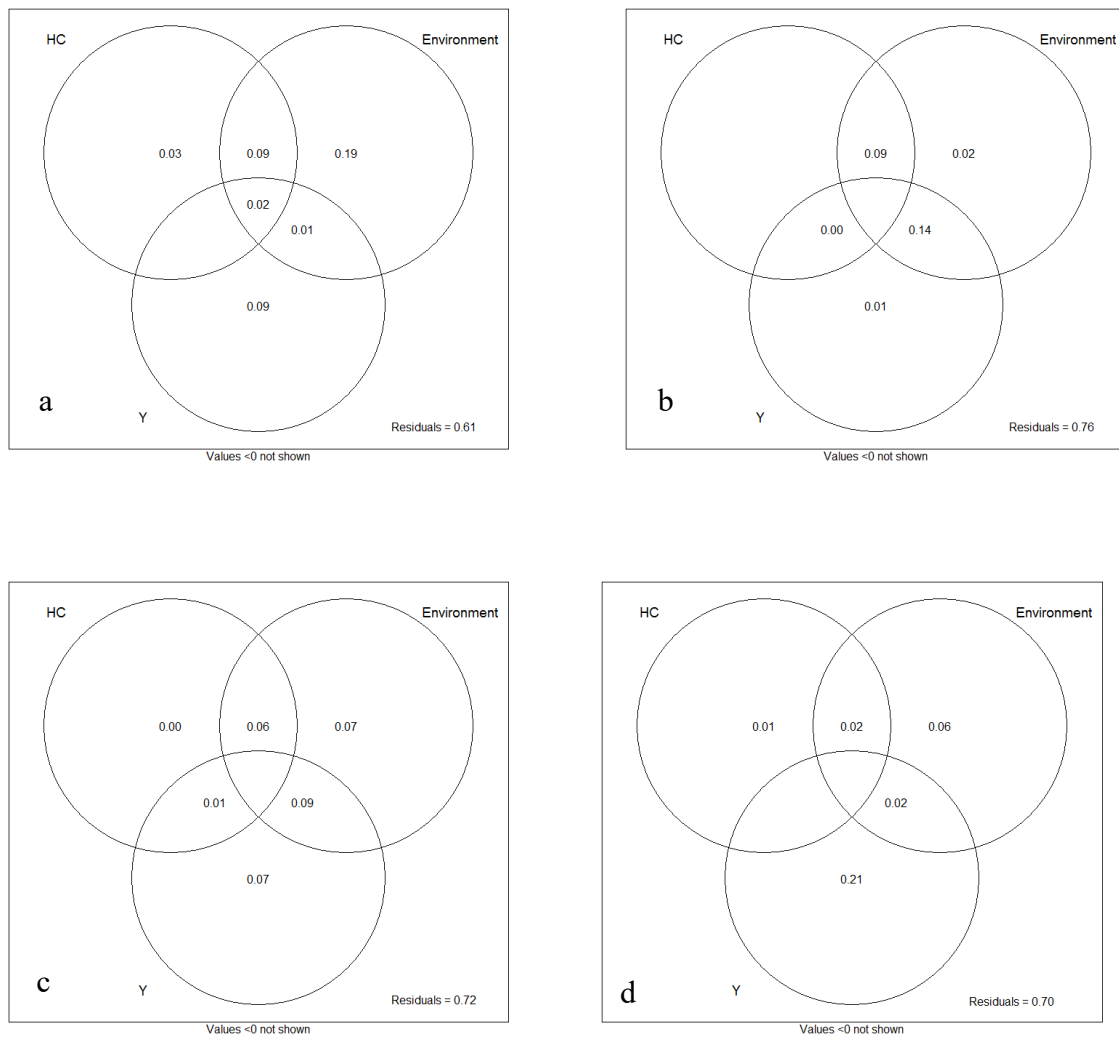
**Figure S2.** Relationship between the distance to the infiltration zone (m) and electrical conductivity.



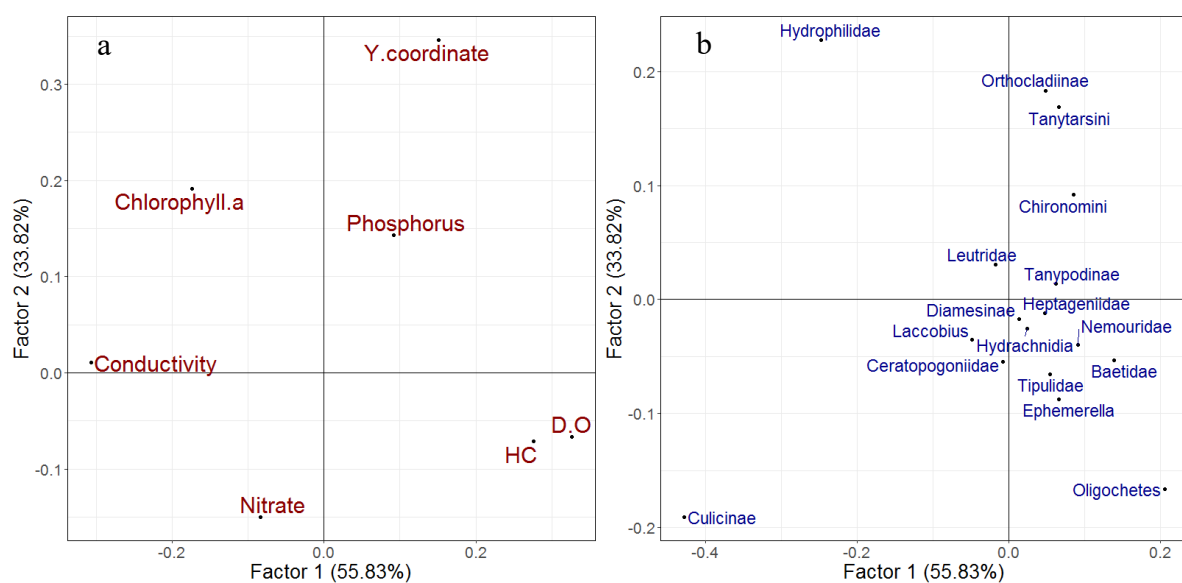
**Figure S3.** Relationship between chlorophyll-a concentration ( $\mu\text{g/L}$ ) and hydrological connectivity measured as  $-1 \times \text{distance to infiltration zone (m)}$ , at Days 15 (a), 20 (b), 30 (c) and 45 (d).



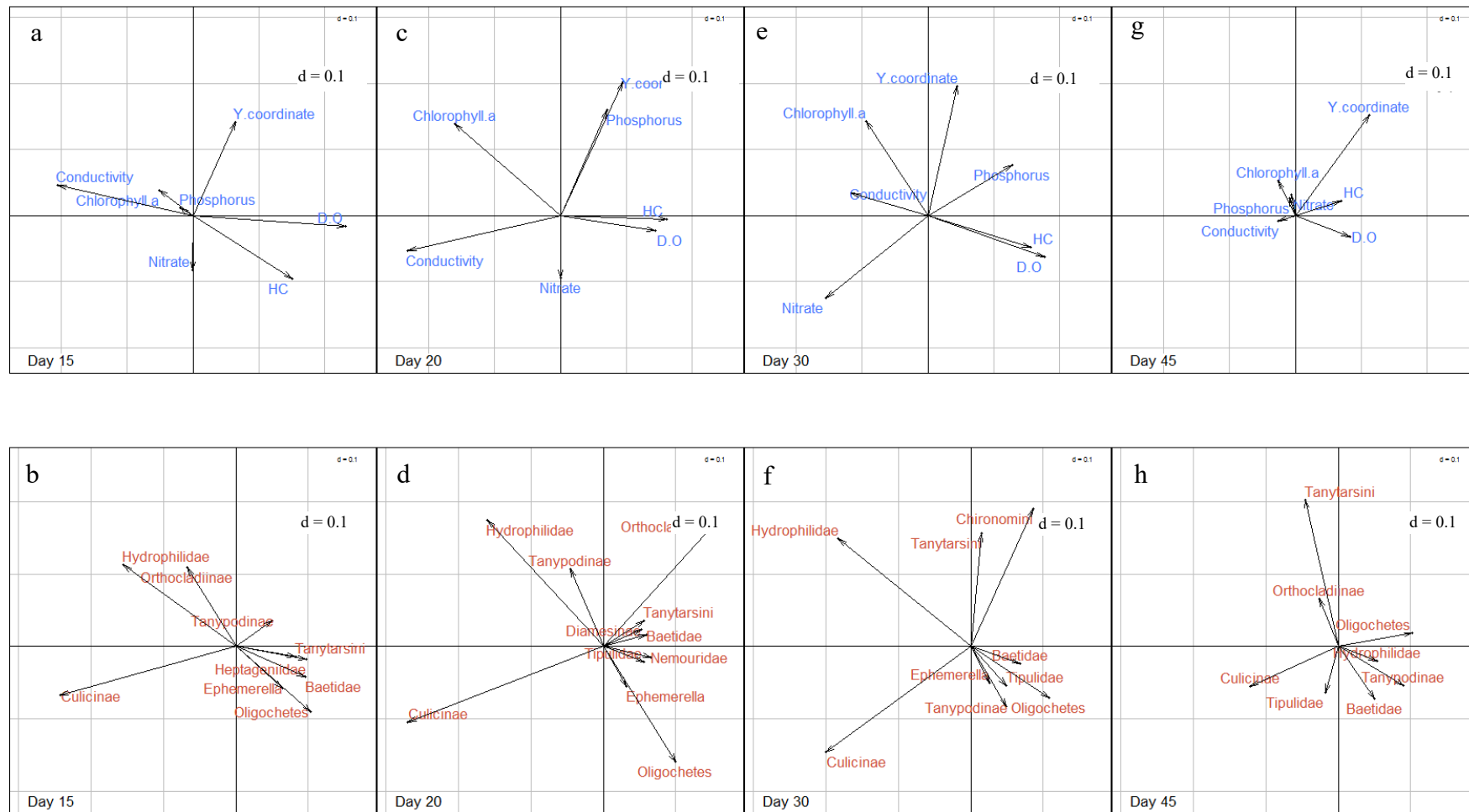
**Figure S4.** NMDS plots for each sampling date, showing the composition of macroinvertebrate communities. Site labels are coloured according to their level of hydrological connectivity.



**Figure S5.** Diagrams showing the results of the variance partitioning at Days 15 (a), 20 (b), 30 (c) and 45 (d).



**Figure S6.** Graphical representation of the compromise produced by the STATICO analysis, with environmental descriptors (a) and species (b) coordinates.



**Figure S7.** Trajectory factor plots of the STATICO analysis. Projection of coordinates of the environmental variables (a, c, e, g) and of species abundances (b, d, f, h) on the first factorial plan at each sampling date. For clarity, species with projections values  $< 0.05$  on both axes of the factorial plan were not displayed.

**Table S1.** Summary of spatial distances (m) among experimental ponds, between ponds and river channel and between ponds and a natural floodplain pond.

<b>Spatial distances</b>	<b>Minimum</b>	<b>Maximum</b>	<b>Median</b>	<b>Mean</b>	<b>SD</b>
Between experimental ponds (m)	3	322	190	153	117
Between experimental ponds and river (m)	6	46	15	17	11
Between experimental ponds and natural floodplain pond (m)	10	305	125	143	119

**Table S2.** Variance explained by PCA axes 1 and 2 and associated loadings of environmental variables at Days 15, 20, 30 and 45.

	Day 15		Day 20		Day 30		Day 45	
	PCA1	PCA2	PCA1	PCA2	PCA1	PCA2	PCA1	PCA2
<b>Variance explained</b>	42.5	25.6	31.7	24.4	37.2	22.9	58.3	21.7
Distance to infiltration zone	-0.55	0.07	-0.53	0.35	-0.53	0.16	-0.46	0.17
Conductivity	-0.54	-0.03	-0.6	0.3	-0.46	0.35	-0.45	0.16
Dissolved Oxygen	0.22	0.55	-0.03	-0.4	0.44	-0.1	0.47	0.12
pH	0.05	0.39	-0.06	-0.53	0.22	0.57	0.05	-0.49
Nitrate	0.32	-0.45	-0.23	-0.45	-0.04	-0.51	0.24	-0.6
Phosphorus	-0.03	-0.58	0.24	0.18	0.48	0.14	-0.29	-0.53
Temperature	-0.5	-0.02	-0.49	-0.32	-0.15	-0.48	-0.46	-0.22



**Table S3.** List of the 9 biological traits and their number of categories used to calculate the functional diversity of aquatic macroinvertebrates.

No.	Biological traits	Number of categories
1	Body size	5
2	Dispersal	4
3	Life duration	2
4	Reproduction	8
5	Locomotion	6
6	Aquatic stage	4
7	Feeding habits	6
8	Respiration technique	3
9	Voltinism	3

**Table S4.** Results of the GLMM assessing the effect of hydrological connectivity on chlorophyll-a concentrations over time.

	<i>p value</i>	<i>R<sup>2</sup><sub>adj</sub></i>		
Overall model	-	0.60		
	<i>p value</i>	<i>Estimate</i>	<i>Std. error</i>	<i>t value</i>
HC	<0.001	-1.01	0.28	-3.55
Date	<0.001	3.97	1.03	3.85
HC:Date	0.50	-0.01	0.02	-0.68

**Table S5.** Taxa richness, community evenness, diversity and abundances at each sampling date.

	<b>Day 15</b>	<b>Day 20</b>	<b>Day 30</b>	<b>Day 45</b>
Total taxa richness	17	17	16	16
Mean taxa richness	8.86	8.70	8.30	9.56
Mean evenness	0.87	0.86	0.86	0.89
Mean Shannon Diversity	1.98	1.95	1.92	2.10
Mean density	260	381	436	477
Total density	5719	8768	10038	10964

**Table S6.** Results of the variation partitioning showing the amount of variation in macroinvertebrate community composition explained by the three categories of explanatory variables: HC, environmental descriptors, and spatial location of the sites at Days 15, 20, 30 and 45. The shared effects represent the overall effects of each variable (including its interaction with other variables).

	Day 15		Day 20		Day 35		Day 45	
	<i>p value</i>	$R^2_{adj}$	<i>p value</i>	$R^2_{adj}$	<i>p value</i>	$R^2_{adj}$	<i>p value</i>	$R^2_{adj}$
Overall model	<b>0.001</b>	0.38	<b>0.003</b>	0.24	<b>0.001</b>	0.28	<b>0.001</b>	0.3
Environment (shared)	<b>0.001</b>	0.30	<b>0.001</b>	0.24	<b>0.004</b>	0.19	0.073	0.09
HC (shared)	<b>0.005</b>	0.11	<b>0.02</b>	0.007	<b>0.048</b>	0.04	0.302	0.01
Y coordinate (shared)	<b>0.026</b>	0.08	<b>0.001</b>	0.15	<b>0.001</b>	0.15	<b>0.001</b>	0.21
Environment	<b>0.008</b>	0.19	0.346	0.01	0.087	0.07	0.127	0.06
HC	0.074	0.03	0.728	0	0.371	0.01	0.302	0.01
Y coordinate	<b>0.004</b>	0.09	0.267	0.01	<b>0.009</b>	0.07	<b>0.001</b>	0.21
Environment & Y	<b>0.005</b>	0.19	<b>0.009</b>	0.16	<b>0.006</b>	0.16	0.105	0.08
HC & Y	0.48	0	0.755	0	0.228	0.02	0.370	0

**Table S7.** Table showing the row coordinates, or contribution of each explanatory variable to axes 1 and 2 of the compromise in the STATICO analysis.

<b>Environmental variables</b>	<b>Axis 1</b>	<b>Axis 2</b>
HC	0.28	-0.07
Conductivity	-0.31	0.01
Nitrate	-0.08	-0.15
Phosphorus	0.09	0.14
DO	0.33	-0.07
Chlorophyll-a	-0.17	0.19
Y.coordinate	0.15	0.35

**Table S8.** Table showing the column coordinates, or contribution of each taxon to axes 1 and 2 of the compromise in the STATICO analysis.

Species	Axis 1	Axis 2
Chironomini	0.09	0.09
Tanytarsini	0.07	0.17
Diamesinae	0.01	-0.02
Orthocladiinae	0.05	0.18
Hydrophilidae	-0.25	0.23
Culicinae	-0.43	-0.19
Tipulidae	0.05	-0.07
Tanypodinae	0.06	0.01
Baetidae	0.14	-0.05
Heptageniidae	0.05	-0.01
Ephemerella	0.07	-0.09
Leuctridae	-0.02	0.03
Nemouridae	0.09	-0.04
Ceratopogoniidae	-0.01	-0.05
Oligochaete	0.21	-0.17
Hydrachnidia	0.02	-0.03
Laccobius	-0.05	-0.04

**Table S9.** Results of the GLMM examining the effect of hydrological connectivity (HC), spatial location of ponds (Y coordinate), and time (days) on the CWM of the traits “Aquatic passive dispersal”, “Aerial passive dispersal”, and “Aerial active dispersal”.  $\Delta AICc$  represents the difference in AICc between the additive and interactive models.

Response and selected model	<i>Variable</i>	<i>p value</i>	<i>Estimate</i>	<i>Std. error</i>	<i>t value</i>	$R^2_{adj}$
<b>Aquatic passive</b>	HC	<b>0.033</b>	1.03	0.45	2.27	0.41
	Y	0.194	0.43	0.32	1.34	
	Time	0.130	-0.03	0.02	-1.53	
<b>Aerial passive</b>	HC	<b>0.025</b>	-1.07	0.45	-2.37	0.31
	Y	<b>0.003</b>	1.05	0.32	3.29	
	Time	<b>0.003</b>	0.08	0.01	3.08	
<b>Aerial active</b>	HC	0.795	-0.13	0.52	-0.26	0.60
	Y	<b>0.01</b>	-1.45	0.37	-3.96	
	Time	0.222	-0.01	0.01	-1.26	

**Table S10.** Results of the GLMM examining the effect of hydrological connectivity (HC), spatial location of the ponds (Y coordinate), and sampling date on functional diversity. HC and Y were divided by 500 and 1000, respectively, for re-scaling purposes.

	<i>p value</i>	<i>R<sup>2</sup><sub>adj</sub></i>		
Overall model	-	0.51		
	<i>p value</i>	<i>Estimate</i>	<i>Std. error</i>	<i>t value</i>
HC	<b>0.004</b>	-61.84	20.76	-2.98
Y	0.08	6.149	3.506	1.75
Date	<b>0.007</b>	0.239	0.084	2.83
HC : Y	<b>0.002</b>	97.16	30.69	3.17
HC : Date	<b>0.06</b>	2.145	0.736	2.91
Y : Date	<b>0.06</b>	-0.363	0.124	-2.93
HC : Y: Date	<b>0.06</b>	-3.169	1.087	-2.91



## Chapter 3

# Temporal shifts in floodplain macroinvertebrate metacommunity structure

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**Short title:** Metacommunity structure in floodplains

**Abstract:** Metacommunity organization can change in time, reflecting changes in habitat connectivity, dispersal and local environmental conditions, but no studies have investigated the effect of flood disturbance on metacommunity structure in floodplain systems. Here, we examined patterns of spatial and temporal beta diversity in 24 parafluvial habitats of the Maggia river floodplain, Switzerland. We also characterized temporal changes in metacommunity organization for groups of macroinvertebrates with differing dispersal abilities. We found that flooding homogenized environmental conditions within sub-sections of the floodplain. We also found that flooding increased beta diversity by redistributing taxa in a stochastic manner within the floodplain, thus disrupting environment - traits linkages. Most importantly, we found that metacommunity organization varied in time, with greater Species Sorting at later stages of assembly for both aerial and aquatic dispersers. Immediately after the flood, Mass Effects dominated for aerial dispersers whereas aquatic dispersers were distributed randomly, this highlighted the fact that dispersal mode had a great effect on temporal changes in metacommunity organization. Our study shows that the balance between the processes structuring metacommunities in highly dynamic ecosystems does vary with environmental conditions, connectivity and the dispersal ability of species, but also importantly with the stage of assembly following a disturbance.

**Key words:** Metacommunity, stream invertebrates, dispersal, floodplain, disturbance

## Introduction

Metacommunities are traditionally defined as an ensemble of local communities linked by the dispersal of multiple, potentially interacting species, where both local interactions and regional processes influence community assembly (Leibold et al. 2004). The main focus of metacommunity research is to bridge local processes and spatial patterns in landscapes (Leibold et al. 2004, Holyoak et al. 2005). Four main metacommunity paradigms were originally described (Neutral theory, Patch Dynamics, Mass Effects and Species Sorting, see Leibold et al. 2004), yet it is now well accepted that metacommunities should rather be described along a continuum between Species Sorting (SS) and Mass Effects (ME) (Cottenie 2005), of which the position may be influenced by the strength of environmental filtering and dispersal rates (Lindström and Lagenheder 2012, Winegardner et al. 2012).

The general view is that SS is the primary structuring force in freshwater communities (Vanschoenwinkel et al. 2007, Waterkeyn et al. 2008, Göthe et al. 2013, Heino et al. 2015). Yet spatial control may also be important, depending on the dispersal ability of species in relation to spatial distances and connectivity levels (Heino et al. 2015, Datry et al. 2016, Thompson and Townsend 2006, Canedo et al. 2015). For instance, the level of hydrological connectivity (HC) within a floodplain or a stream network can have a large effect on aquatic dispersal rates and therefore on metacommunity structuring, especially for aquatic dispersers (Gallardo et al. 2008, Brown and Swan 2010, Fernandes et al. 2014, Petsch et al. 2017, Sarremejane et al. 2017a). Similarly, macroinvertebrates with an aerial active dispersal mode may experience greater spatial control, as a result of ME in floodplains or stream networks, compared to aquatic or passive dispersers (Tonkin et al. 2016, Sarremejane et al. 2017a).

In highly disturbed freshwater ecosystems, such as alluvial floodplains and intermittent rivers, the factors influencing the metacommunity structure (local environmental conditions and connectivity levels) may greatly vary in time, and this can result in temporal shifts in the processes structuring metacommunities (Fernandes et al. 2014, Datry et al. 2016, Sarremejane et al. 2017b). In streams and floodplains, spatial control on communities tends to increase during high flows, reflecting local homogenization (Sarremejane et al. 2017b, Chaparro et al. 2018), although other studies in floodplains have shown that Species Sorting dominates during long inundation periods when aquatic species are released from dispersal limitation and can track environmental variation (Dias et al. 2016, Fernandes et al. 2014).

Floodplain systems are particularly well-suited to studying the temporal shifts in metacommunity structure, because the factors known to potentially affect metacommunity organization, such as local abiotic conditions, level of hydrological and landscape connectivity (distances to potential sources of colonists) and disturbance regime can vary spatially amongst parafluvial habitats, and also in time (Amoros and Bornette 2002, Brunke et al. 2003, Stanford et al. 2005, Opperman et al. 2010, Capderrey et al. 2013). Local conditions vary with the level of lateral connectivity to the main channel and vertical connectivity with alluvial aquifers, both of which can be pulsed or constant over time (Amoros and Bornette 2002, Brunke et al. 2003, Opperman et al. 2010, Capderrey et al. 2014). The most frequently flooded habitats (high HC) typically exhibiting abiotic conditions rather similar to the main channel, and the more rarely flooded habitats (low HC) leaning towards ponds conditions (Amoros and Bornette, Paillex et al. 2009). Floods quickly homogenize environmental conditions and local communities among parafluvial habitats (Thomaz et al. 2007, Sarremejane et al. 2017b, Chaparro et al. 2018), and

conditions may then diverge over time, depending on their position within the floodplain and different properties in ecological succession (Thomaz et al. 2007). The gradient in inundation frequency and associated environmental responses is known to strongly affect invertebrate community structure (Gallardo 2008, Paillex et al. 2013, Fernandes 2014, Gallardo 2014) and, to a lesser extent, functional trait distributions (Paillex et al. 2009, Gallardo et al. 2014).

Functional traits, as variables describing biological attributes of species (Resh et al. 1994, Statzner and Bêche 2010) can be very useful in understanding processes structuring communities (Mondy and Usseglio-Polatera 2013, Townsend and Hildrew 1994, Townsend et al. 1997). Specifically, traits distribution along the HC gradients could reflect changes in voltinism (Townsend and Hildrew 1994, Gallardo et al. 2008, Sheldon et al. 2010), feeding mode (Merritt et al. 2002, Paillex et al. 2009), respiratory and reproductive modes (Gallardo et al. 2008). Functional homogenization along environmental gradients may also help understanding their effects on communities, because abiotic stress typically reduces community specialization (Mondy and Usseglio-Polatera 2013). Despite our understanding of the functioning of floodplain systems, much remains unknown regarding the role of dispersal in these complex systems, and especially how it varies in time. We argue that to really capture the broad patterns of metacommunity structuring in floodplains, the relative importance of environmental and spatial factors must be examined in a temporal framework including flood events.

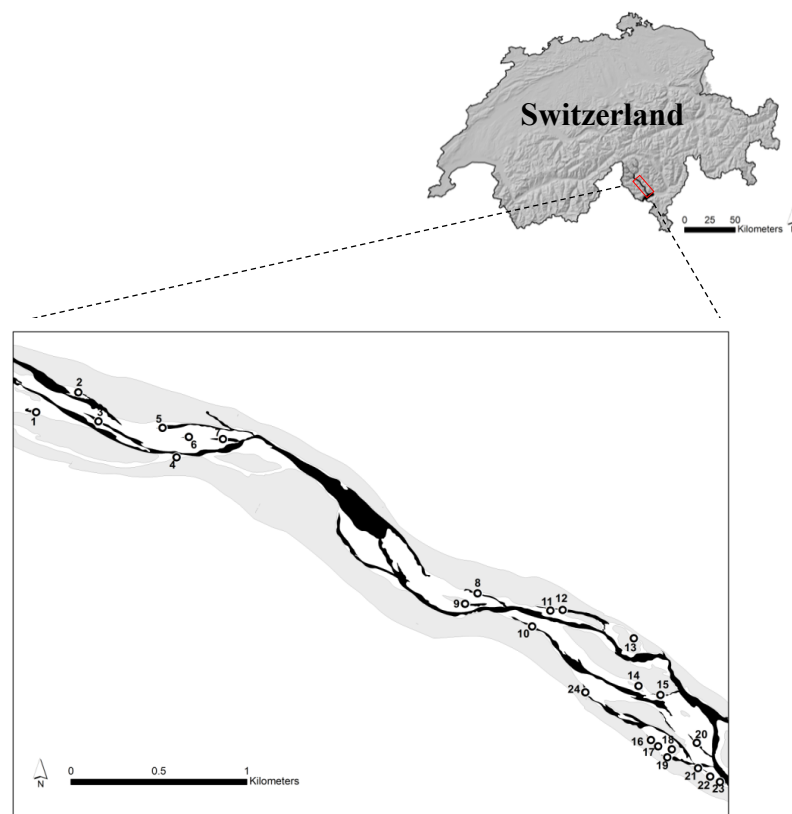
Here we investigated temporal changes in metacommunity patterns among in 24 parafluvial floodplain habitats (PFH) following a large flood. We specifically asked how local environmental conditions and spatial factors (including the level of landscape connectivity) interacted to determine metacommunity patterns in parafluvial habitats, and whether these factors had an effect on temporal stability of local communities. Last, using functional traits, we examined functional homogenization along the main environmental gradients and explored the environmental selection of species and the trait-environment relationships. We tested two main hypotheses: H<sub>1</sub>: Flooding would reset and homogenize environmental conditions and communities within the floodplain thus disrupting environment-biota relationships. H<sub>2</sub>: Immediately after the flood, aerial dispersers would be able to recolonize where landscape connectivity is high, whereas aquatic dispersers would have more homogeneous distributions, over time, species sorting would then increase for both dispersal groups. These two hypotheses lead to specific pattern predictions: Beta diversity and environmental variation should be lowest immediately after flood. Environment-trait linkages would be weak after the flood. Overall, SS would dominate metacommunity organization, reflected in high turnover between local communities. Finally, spatial control would be higher for aerial dispersers immediately after the flood, whereas environmental control would especially affect aquatic dispersers at later stages of assembly.

## **Methods**

### *Study Area*

The Maggia river is located in the south-eastern part of the Swiss Alps and flows southward into Lake Maggiore (Figure 1). It is one of the last remaining natural (non-urbanized) floodplains in Switzerland, and therefore has been declared a site of national importance (Kuhn and Amiet 1988). Its catchment covers an area of 930 km<sup>2</sup> with elevations

ranging from 200 to 3300 m a.s.l. Owing to the presence of two glaciers in the headwaters and snowfall precipitation in winter, the hydrological regime is classified as glacionival. Following the construction of a complex hydropower scheme in the headwaters in 1953, the flow regime of the river has been substantially modified (Pfamatter and Zanetta 2003, Molnar et al. 2008). The original high flows during snowmelt have been replaced by essentially constant flows (minimum flow requirements  $\sim 1.5 \text{ m}^3/\text{s}$  in Bignasco upstream from the floodplain) with occasional flood peaks with no correlation between magnitude and return period (Molnar et al. 2008, Perona et al. 2009). The alluvial floodplain used in this study is located in the middle of the valley; it is about 7-km long and nearly 2-km wide in some sections. Because of the fairly low storage of the hydropower scheme and high lateral hillslope runoff during major rain events, the largest flood peaks still occur but the lesser magnitude floods do not. The combination of high flows and an abundance of bedload sediment (mean diameter of stones = 120 mm) maintains a diverse floodplain habitat. Within the floodplain, single-thread sections alternate with braided reaches where various types of parafluvial habitats occur: ponds, connected and disconnected side arms, and backwaters. For this study, we selected 24 permanently-wetted parafluvial habitats, specifically permanent ponds, disconnected side arms, and side arms connected at their downstream end with a shallow riffle.



**Figure 1.** Map of Switzerland showing the location of the Maggia River floodplain and the parafluvial habitats sampled.

#### *Sampling and laboratory analysis*

We visited each site on 6 dates in 2016: May 11<sup>th</sup>, June 27<sup>th</sup>, July 11<sup>th</sup>, July 27<sup>th</sup>, August 15<sup>th</sup> and September 13<sup>th</sup>. A relatively large flood occurred on June 16<sup>th</sup> (discharge =  $478 \text{ m}^3/\text{s}$ ,

return period = 0.79), and we were therefore able to compare environmental conditions, and macroinvertebrate communities before and after the flood, then follow developments until September. On each visit, a water sample (0.5 L) was collected from each habitat and stored on ice in the dark for chemical analysis in the laboratory. In the laboratory, water samples were analyzed for nitrate (NO<sub>3</sub>, mg/L), and pH using standard methods following Tockner et al. (1997). Spot measurements of dissolved oxygen (mg/L, Hach HQ40d connected to a LD10101 oxygen probe), water temperature (°C), and electrical conductivity (µS/cm, WTW meter, Germany) also were taken on each visit. Particulate organic matter (CPOM) was collected at 3 locations within each habitat using a Hess sampler (250 µm mesh, 0.04 m<sup>2</sup> area), by disturbing the substrate to a depth of ~ 10 cm, and the collected POM was preserved frozen. Once in the laboratory, POM was thawed, then dried at 60°C for 24h, weighed, then combusted at 450°C for 6h and reweighed for estimates of biomass as AFDM. At each sampling event, the order in which water samples and physico-chemical variables were measured was randomized among ponds to reduce bias of collection time. Substrate size composition was measured using the zig-zag pebble count method where 50 cobbles were randomly selected along a reach and their b-axis measured (Bevenger and King 1995). The structural diversity of the substratum within each habitat was calculated using the Shannon-Wiener index H (Cellot et al. 1994, Burnett et al. 1998, Brunke et al. 2003):

$$H = - \sum_{i=1}^S (p_i \ln(p_i))$$

With S being the number of Wentworth substrate size classes (Wentworth et al. 1922, Table S1 in supporting information) and p<sub>i</sub> the proportion of the total sample belonging to the i<sup>th</sup> size class. We developed a 2D hydrodynamic model for the floodplain and used it to translate river discharges into inundation patterns within the floodplain. We were therefore able to calculate a flooding frequency for each habitat between March 2014 and each of our sampling dates. Note that flooding frequencies were the same at each date, because only one flood occurred during our study and inundated all habitats. The model was developed with the Basement software (Faeh et al. 2010, developed at ETH Zurich: <http://www.basement.ethz.ch/>), and a detailed description of the modelling process is described in Chanut et al. (in review).

Benthic macroinvertebrates were randomly collected (n = 3, at each site and date) using a Hess sampler (250 µm mesh, 0.04 m<sup>2</sup> area) and preserved in 70% ethanol. In the laboratory, collected individuals were hand-picked, counted and identified to the lowest possible taxonomic level using Tachet et al. (2010).

*Trait data-* For the analysis of the relationships between the environment and species traits, we identified a set of functional traits that we predicted could be influenced by the main environmental gradients and by the flood. Specifically, we selected traits describing the feeding, locomotion and respiratory modes as well as the life cycle duration, voltinism and the type of eggs laid. This amounted to 19 categories distributed in 6 biological traits (Table 1). Functional traits for all taxa were obtained from the Tachet database for each taxon (Tachet et al. 2010), this database provides an affinity of a given taxa for a particular trait class using a fuzzy coding approach ranging from 0 for low affinity to 3 for high affinity. To give the same

weight to all traits, affinity scores were standardized so that their sum for a given taxon would equal 1 (see Paillex et al. 2013).

**Table 1.** List of the 6 biological traits and their trait classes used in the analyses of community specialization and trait-environment linkages, and dispersal-related trait classes used to partition species in aerial or aquatic dispersers. Abbreviations are used in the graphical representations.

Trait	Trait class	Abbreviation
Life cycle duration	< 1 year	Short_LC
	>1 year	Long_LC
Potential number of reproductive cycles per year	<1	Univ.
	>1	Pluriv.
Reproduction	isolated eggs, free	Isol.free
	isolated eggs, cemented	Isol.fixed
	clutches, cemented or fixed	Clutches.fixed
Respiration	clutches, free	Clutches.free
	tegument	Resp_tegt
	gill	Resp_gill
Locomotion and substrate relation	spiracle (aerial)	Resp_spir
	full water swimmer	Full_water
	crawler	Crawler
	burrower	Burrower
Feeding habits	temporary attached	Attached
	shredder	shredder
	scraper	Scraper
	Deposit feeder	Depos_feeder
Dissemination	predator	predator
	Aquatic passive	-
	Aquatic active	-
	aerial passive	-
	aerial active	-

#### Data analysis

*Temporal changes in local environmental conditions* - To test the part of H<sub>1</sub> positing that parafluvial habitats would differ in environmental conditions, we used a PCA on physico-chemical attributes: DO (mg/l), water temperature (°C), electrical conductivity (μS/cm), pH, nitrate concentration (mg/l), CPOM biomass (g/m<sup>2</sup>), substrate structural diversity, the median sediment size D50 (cm) and flooding frequency (floods/year). To address H<sub>1</sub>, regarding the homogenizing effect of flooding on habitat conditions, we tested whether the variability in local environmental conditions among sites differed between dates, for that we used the betadisper function from the vegan package on the euclidean distance matrix. We used a permutation test with 999 permutations to test for differences in dispersion between dates, when significant a pairwise permutation test was conducted to specifically examine differences between individual dates. In order to examine whether environmental conditions were different between dates, we used a PERMANOVA on a Euclidean distance matrix on the same set of environmental attributes, using the adonis function of the vegan package. If the results of the



PERMANOVA were significant, we conducted a pair-wise PERMANOVA to test significant differences between dates, using the `pairwise.perm.manova` function from the `RVAideMemoire` package.

*Diversity patterns and partitioning of beta diversity* – Similarly, we tested whether flooding would homogenize communities. For this, we calculated beta diversity as the distance to group centroid based on Chao distances on abundance data, with the `betadisper` function from the *vegan* package. We chose the Chao index over the commonly used Bray-Curtis distance because it handles unequal sample sizes more efficiently, and here not all sites were present at all dates (Canedo et al 2015). We used a permutation test with 999 permutations to test for differences in beta diversity between sampling dates, when significant a pairwise permutation test was conducted to specifically examine differences between individual dates. We then also tested whether the overall community structure (i.e. the position of the centroid in non-dimensional species space for each date) changed between dates with a PERMANOVA, using the `adonis` function of the *vegan* package.

To assess whether beta diversity was more structured by turnover and nestedness, we partitioned beta diversity in its nestedness and turnover component following Baselga (2010) based on presence-absence data. We then tested whether these partitions were greater than expected by chance by comparing them with null matrix. Following Tonkin et al. (2016), we used the `oecosimu` function based on 10 000 permutations to create the null matrices, constrained with the R1 method (fixed-incidence proportional) and the `nestedbetasor` function to partition beta diversity. This method returns statistics describing whether the observed partitions are greater than expected by chance alone.

Finally, we tested whether taxa richness, community evenness and temporal stability varied along the main environmental gradient. For that, we calculated temporal turnover in community composition between consecutive dates with the `beta.temp` function of the *betapart* package, based on presence-absence data. First, we averaged the temporal beta diversity values across all sites and examined the overall turnover between each consecutive date, here we tested whether the temporal turnover differed between pairs of consecutive dates using a one-way ANOVA and a Tukey's HSD test to assess pairwise differences if the ANOVA was significant. Then we averaged the values across all dates for each site and tested whether temporal turnover was affected by environmental conditions and landscape connectivity. For that, we used a stepwise forward selection based on AIC criterion where the potential pool of explanatory variables contained all time-averaged environmental descriptors as well as all structural connectivity metrics. The effect of the variables retained in the forward selection procedure was then tested with a linear regression model. Finally, we assessed changes in taxa richness and community evenness through time and along the environmental gradient. We started by examining how landscape connectivity and environmental conditions affected taxa richness and community evenness, using a forward selection based on AIC criterion, including all the landscape connectivity variables, and the first and second axes of the PCA on environmental variables. The linear model used was a GLMM and because of the repeated-measure structure of our dataset, we included site ID as a random effect the model to account for unmeasured site-specific effects, and the sampling date was included as fixed factor to correct for temporal effects. We used the `stepAIC` function from the *MASS* package for variable selection. We then tested whether taxa richness and community evenness significantly differed between dates

using one-way ANOVA, and when significant we tested for differences between individual dates using a post hoc Tukey's HSD test.

*Spatial and Connectivity variables* – In order to assess the level of spatial control on metacommunity organization, we first calculated a set of variables describing spatial distances amongst habitats and the level of LC. The spatial component consisted Principal Coordinates of Neighbourhood Matrix (PCNM). The PCNM approach (Borcard and Legendre 2002, Borcard et al. 2004) constructs a set of orthogonal vectors representing different scales of spatial variation within a system, thereby maximizing the information provided by spatial coordinates. These vectors then can be used as separate variables describing different scales of variation. Seven independent PCNM vectors representing positive spatial autocorrelation were generated. Two LC metrics were calculated: the distance to nearest neighbouring parafluvial habitat and a modified version of the “*Ti metric*” (Theobald et al. 2011, Fernandes et al. 2014):

$$Ti = \sum_{j=1}^n w_{ij} / (A_j \times A_i)$$

Where  $w_{ij}$  is the spatial distance between patches  $i$  and  $j$ , and  $A_j$  and  $A_i$  the respective surface areas of patches  $i$  and  $j$ . High values of  $Ti$  suggest more isolation. We calculated the metric using surface area of the patches rather than their depth, because parafluvial habitats in the Maggia floodplain are relatively shallow and rather benthic than pelagic ecosystems. Additionally, we examined benthic macroinvertebrate communities, surface area is therefore a better proxy for ecosystem size than water depth or volume in that particular case, which contrasts with the study of Fernandes et al. (2014) which examined pelagic fish species.

*Variance partitioning* – In order to tests  $H_2$ , we examined the temporal changes in the relative influences of environmental, spatial and connectivity variables on the structure of the macroinvertebrate communities, using partial redundancy analysis based on Bray-Curtis distances at each date. Because community composition was affected by the influence of a few highly abundant taxa, macroinvertebrate abundances were Hellinger-transformed to increase the resolution for changes in community structure. Partial redundancy analysis partitions the effects of each explanatory matrix into its pure effect (independent of other variables) and its shared effects with other matrices. We used the varpart function from the *vegan* package. The amount of variation explained by each matrix was assessed using the adjusted  $R^2$  and the significance of each fraction was also tested separately. Prior to conducting the variance partitioning, a forward selection procedure based on AIC criterion was used on each explanatory matrix to select the most influential variables (Devercelli et al. 2016, De Campos et al. 2018). In order to remove highly multicollinear variables, we sequentially removed the variables with a variance inflation factor (VIF) greater than 10, starting from the variable with the greater VIF (Tonkin et al. 2016).

In order to assess the influence of dispersal ability on metacommunity organization, we separated the communities in primarily aerial dispersers and primarily aquatic dispersers. For that, we followed Tonkin et al. (2016), and all taxa with a score for “aerial active dispersal” greater than 3 were categorized as aerial dispersers, all other taxa were classified as aquatic dispersers. We then completed the variance partitioning procedure separately for aerial dispersers and aquatic dispersers.

*Temporal variation in environmental filtering of traits* – Finally, to test our prediction that trait-environment linkages would be weakest after the flood, we first calculated a

community-level weighted mean (CWM) for each trait class, which is the mean trait value of all species present in the community, weighted by their relative abundances. We used the *dbFD* function from the *FD* package in R (Laliberté and Legendre, 2010). We first averaged all CWM across sites for each date and examined the temporal variations between dates. We then used a STATICO analysis (Simier et al. 1999, Thioulouse et al. 2004) to examine the temporal stability in trait-environment linkages. Data was organized into a succession of coupled tables of environmental descriptors and CWM, each pair of tables corresponding to a sampling date. The STATICO method is a combination of the co-inertia analysis (Doledec and Chessel, 1994) and the Partial Triadic Analysis (Thioulouse and Chessel 1987). It proceeds in three stages: the first stage analyses each table one-by-one with PCA; the second stage consists in linking each pair of tables (a pair for each date) by co-inertia in order to find axes that maximize covariance between row coordinates of species and environment matrices; finally, a partial triadic analysis is used to analyze the sequence of cross-covariance tables and produces a compromise, or mean species-environment co-structure for all dates. STATICO allows the graphical representation of the projection of the sites (in the original species and environmental tables) on the compromise axes, and thus a straightforward analysis of temporal change in species-environment linkages. The analysis and plotting were conducted on R with the *ade4* (Thioulouse et al. 1997) package.

To assess community homogenization along the main environmental gradients, we started by calculating a community specialization index following Mondy and Usseglio-Polatera (2004). This consisted in first calculating a specialization index for each taxon and trait:

$$TSI_{ti} = \sum_{k=1}^h C_{tik}^2$$

With  $TSI_{ti}$  the specialization score for taxon  $t$  and trait  $i$ , and  $C_{tik}$  the relative use of category  $k$  of trait  $i$  by taxon  $t$ , with  $(1 \leq k \leq h)$ . This score was then adjusted to take into account the different number of classes  $k$  in each trait  $i$ :

$$TSI.adj_{ti} = (TSI_{ti} - \min_{TSI}) / (\max_{TSI} - \min_{TSI})$$

With  $\min_{TSI} = 1/k$  and  $\max_{TSI} = 1$ . Finally, for each of the traits, we calculated a community specialization index, which we later averaged across traits to obtain an average score for community specialization. The community specialization index for each individual trait was calculated as follows:

$$CSI.adj_i = \sum_{t=1}^N (TSI.adj_{ti} \times a_t) / \sum_{t=1}^N a_t$$

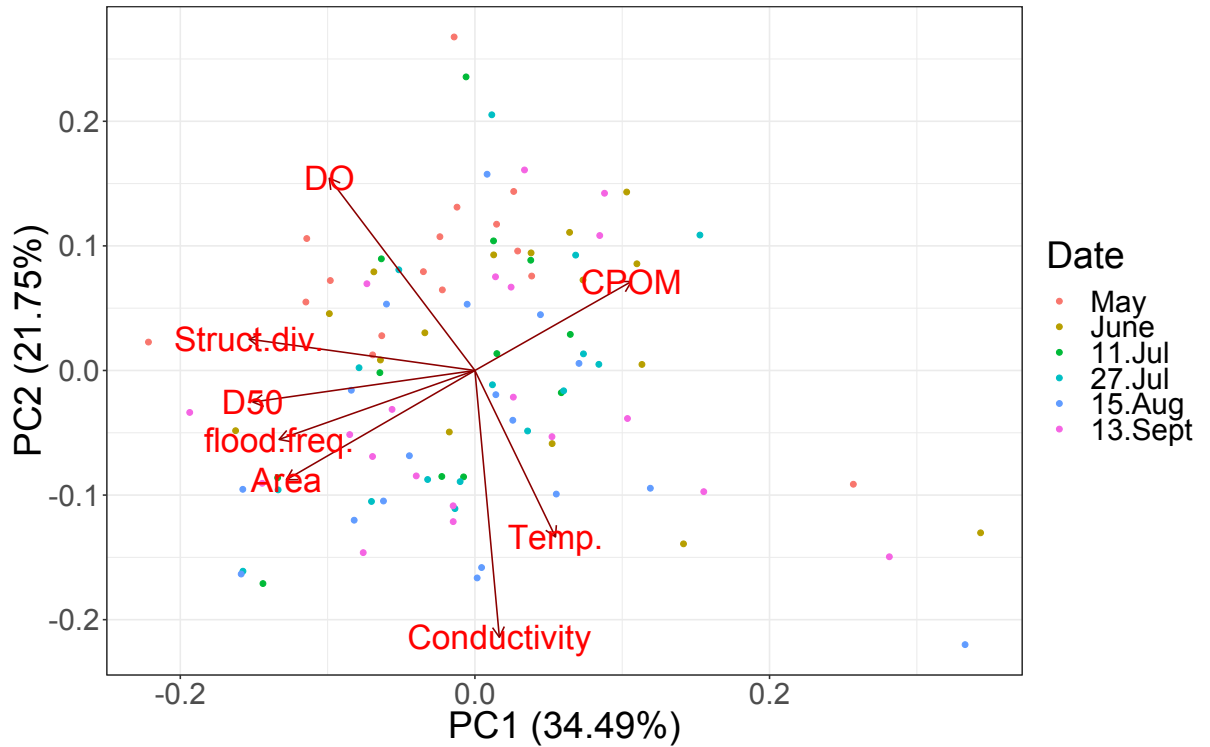
Where  $a_t$  is the abundance of taxon  $t$ , with  $(1 \leq t \leq N)$ . We used a GLMM with site ID as a random effect and the first and second axes of the PCA on environmental variables and the sampling date as a fixed effect to assess the effect of the environmental gradient on community specialization.

## Results

### *Temporal changes in local environmental conditions*

PCA1 explained 34.5% of the total variation in on physico-chemical attributes and described the opposition between frequently-flooded habitats with high structural diversity,

sediment size, DO levels and surface area and habitats with high CPOM biomass and high-water temperature (Figure 2). PCA1 represents the gradient of flooding frequency and resulting environmental variation. PCA2 explained 21.8% of total variation and segregated habitats according to their high DO levels on the positive side and high electrical conductivity and high water temperature on the negative side. This axis may represent the differences in water origins within the floodplain (e.g. deep groundwater, shallow groundwater, terrace aquifer exfiltration, river water).

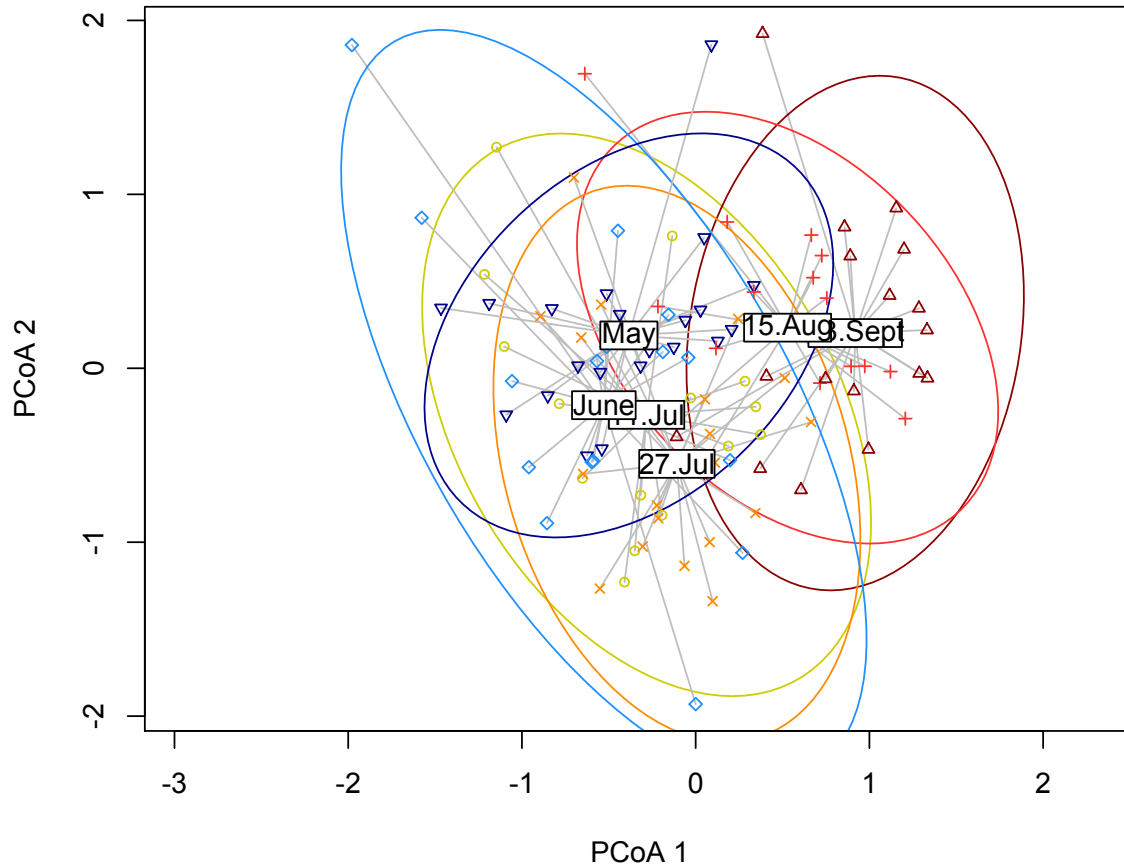


**Figure 2.** Biplot of the principal component analysis conducted on environmental variables: DO (mg/l), water temperature (°C), electrical conductivity (μS/cm), pH, nitrate concentration (mg/l), CPOM biomass (g/m<sup>2</sup>), substrate structural diversity (“Struct.div”), the median sediment size D50 (cm) and flooding frequency (“flood.freq”, floods/year).

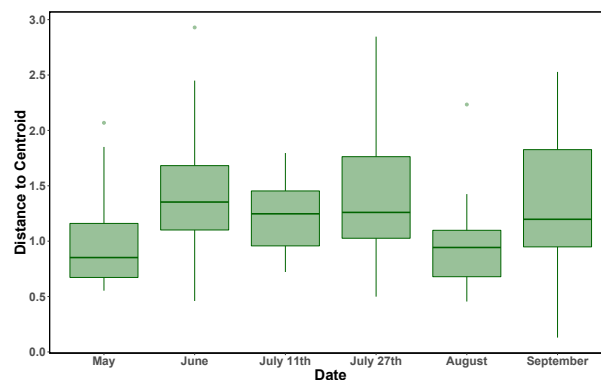
The dispersion of environmental conditions (measured as the distance to centroid) varied significantly between dates ( $F = 3.11$ ,  $p = 0.02$ ). Specifically, it increased significantly between May and June ( $p = 0.014$ , from 1.56 to 2.6) and decreased significantly from June to July 11 (0.01, from 2.6 to 1.54). The PERMANOVA showed that local environmental conditions differed significantly between sampling dates ( $p = 0.001$ ,  $R^2 = 0.25$ ,  $F = 6.045$ ). Specifically, differences were significant between May and June ( $p_{\text{adj}} = 0.015$ ,  $R^2 = 0.27$ ,  $F = 10.96$ ), between July 27 and August ( $p_{\text{adj}} = 0.015$ ,  $R^2 = 0.14$ ,  $F = 5.24$ ) and between August and September ( $p_{\text{adj}} = 0.015$ ,  $R^2 = 0.13$ ,  $F = 5.63$ ).

### *Diversity patterns and partitioning of beta diversity*

Beta diversity varied significantly between dates ( $F = 2.72$ ,  $p = 0.016$ ), with a significant increase between May and June (from 0.97 to 1.43,  $p = 0.01$ ) and a decrease between July 27 and August 15 (Figures 3 and 4 from 1.34 to 0.97,  $p = 0.028$ ). The PERMANOVA results showed that communities were significantly different between dates ( $p = 0.001$ ,  $R^2 = 0.19$ ,  $F = 5.02$ ), and specifically between July 27 and August 15 ( $p_{\text{adj}} = 0.015$ ,  $R^2 = 0.11$ ,  $F = 4.74$ ).



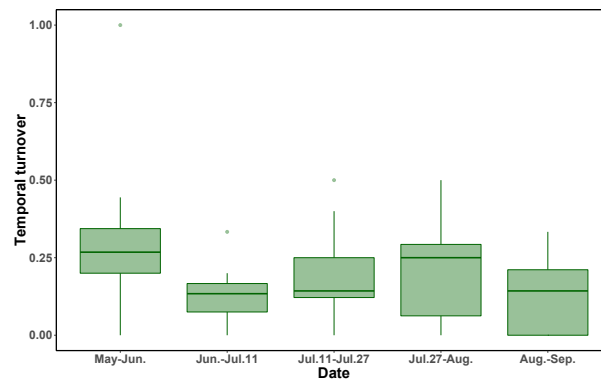
**Figure 3.** Results of the betadisper analysis, showing the dispersion of sites around the centroid for each date, based on Bray-Curtis distance of species abundances. May in dark blue, June in light blue, July 11 on green, July 27 in orange, August 15 in red and September 13 in brown.



**Figure 4.** Boxplots showing the distributions of distances to centroid for each date. Letters represent the significant differences between pairs of consecutive dates, with a same letter signifying that the values are significantly different between these two dates.

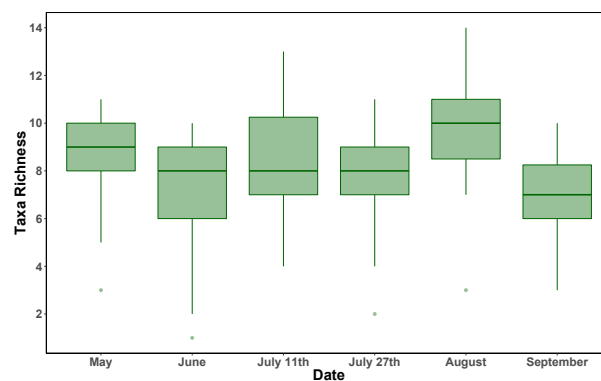
At all dates, the partitioning of beta diversity and comparison to null model showed that beta diversity and species turnover were significantly lower than expected by chance, whereas nestedness was higher than expected by chance (Table S2, Supporting Information). Temporal turnover in community composition averaged 0.18 and was highest between May and June (0.29) and lowest between August and September (0.1, Figure 5).

There was a significant difference in temporal turnover between pairs of consecutive dates ( $p = 0.018$ ,  $R^2 = 0.09$ ,  $F = 3.15$ ), with significantly higher turnover between May and June than between June and July 11 ( $p = 0.004$ ) and between August and September ( $p = 0.02$ ). Average values of temporal turnover for each site were not significantly affected by local environment nor landscape connectivity.

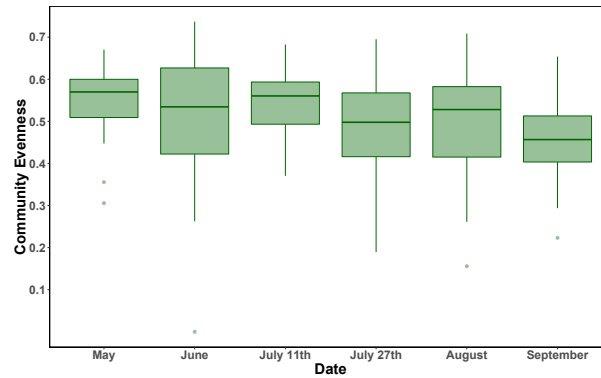


**Figure 5.** Boxplots showing the temporal turnover in species composition between consecutive dates.

Taxa richness was lower at sites with lower hydrological connectivity, but this trend was non-significant ( $p = 0.051$ ). When compared between dates, average taxa richness was significantly higher on August 15 compared to June and to September (Figure 6,  $F=3.62$ ,  $p = 0.046$ ). Finally, community evenness did not vary significantly between dates ( $F = 1.68$ ,  $p = 0.146$ ) and was unrelated to environmental conditions or landscape connectivity (Figure 7).



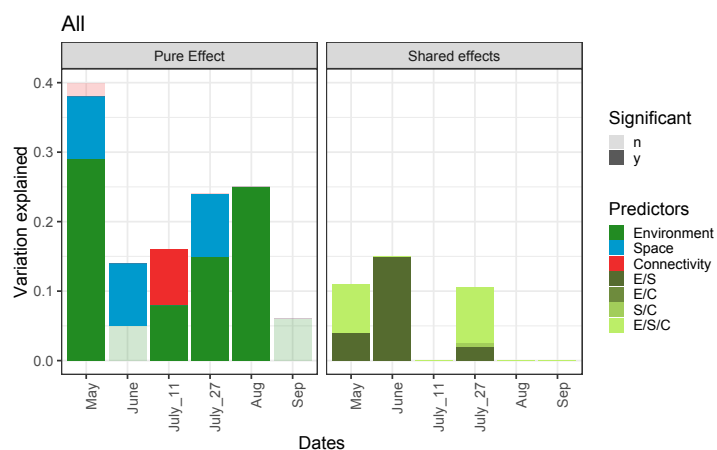
**Figure 6.** Boxplots showing the distributions of taxa richness at each date. Letters represent the significant differences between dates, with a same letter signifying that the values are significantly different between these dates.



**Figure 7.** Boxplots showing the distributions of community evenness at each date.

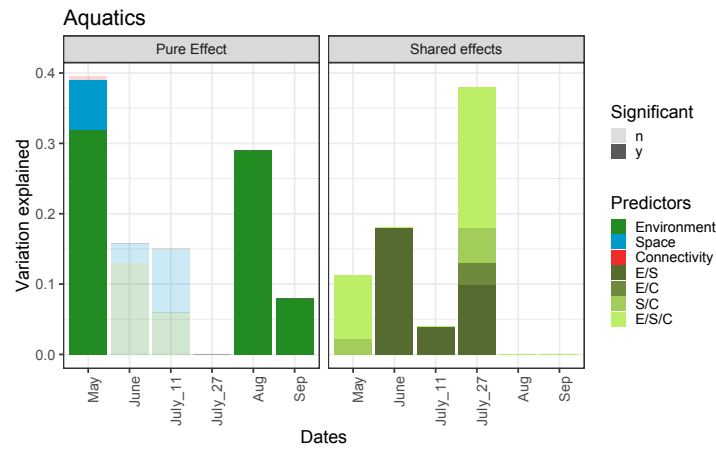
### *Variance partitioning*

Overall, variation in community structure was best explained in May (residuals = 0.54). Local environment explained the most variance in community structure in May, July 11, July 27 and August (0.29, 0.08, 0.15 and 0.25 respectively). Spatial variables had a small but significant effect in May, June and July 27, and their shared effect with local environment was highest in June (0.15). Structural connectivity had no significant effect except on July 11 (Figure 8). When considering only aquatic dispersers, the community structure was primarily constrained by environmental variables, and their pure effects were highest in May and August (0.32 and 0.29, respectively, Figure 9). Shared effects between environment and space were relatively high in June (0.18) and the shared effects between environment, space and connectivity were high on July 27 (0.2). No pure effect was significant in June, July 11 and July 27, but the overall effects (pure effects + shared effects) of environment and space were significant at these three dates and that of connectivity on July 27. For aerial dispersers, the effect of local environment was relatively high in May and July 27 (0.23 and 0.22, respectively, Figure 10), and the effect of spatial variables was high on July 27. Interestingly, the pure effect of connectivity was high in June and on July 11 (0.16 and 0.16, respectively).

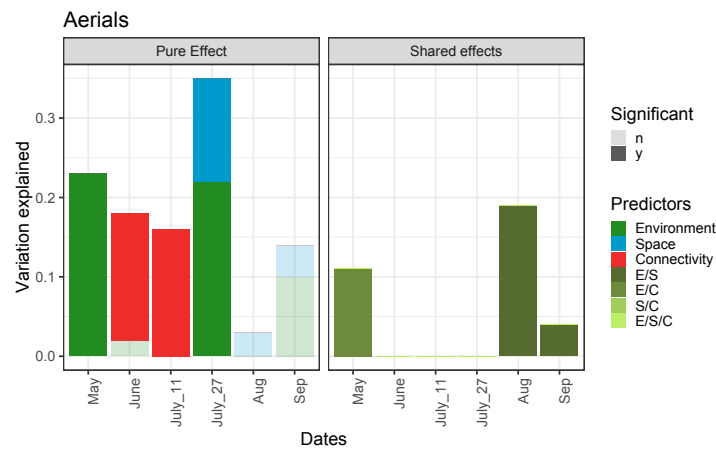


**Figure 8.** Histograms showing the proportion of overall variation in community composition explained by environmental variables, spatial variables and the level of landscape connectivity. Left panel describes the pure effects of each explanatory matrix, the right panel describes the shared effects between matrices: Environment + Space (E/S), Environment + Connectivity

(E/C), Space + Connectivity (S/C) and Environment + Space + Connectivity (E/S/C). Non-significant pure effects are in lighter shade. The significance of shared effects cannot be tested.



**Figure 9.** Histograms showing the proportion of overall variation in aquatic dispersers community composition explained by environmental variables, spatial variables and the level of landscape connectivity. Left panel describes the pure effects of each explanatory matrix, the right panel describes the shared effects between matrices: Environment + Space (E/S), Environment + Connectivity (E/C), Space + Connectivity (S/C) and Environment + Space + Connectivity (E/S/C). Non-significant pure effects are in lighter shade. The significance of shared effects cannot be tested.



**Figure 10.** Histograms showing the proportion of overall variation in aerial dispersers community composition explained by environmental variables, spatial variables and the level of landscape connectivity. Left panel describes the pure effects of each explanatory matrix, the right panel describes the shared effects between matrices: Environment + Space (E/S), Environment + Connectivity (E/C), Space + Connectivity (S/C) and Environment + Space + Connectivity (E/S/C). Non-significant pure effects are in lighter shade.

#### *Temporal variation in environmental filtering of traits*

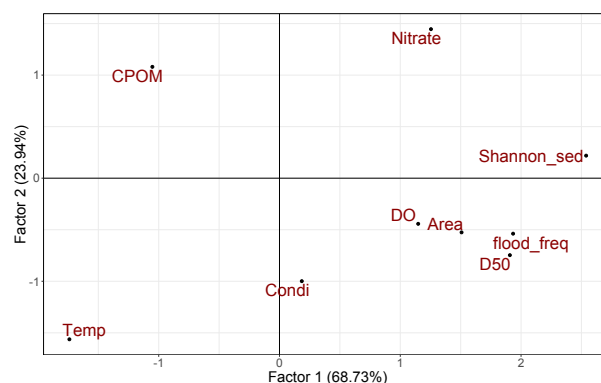
*Temporal stability in trait-environment linkages* - The STATICO analysis showed that statistically significant co-structure between environmental descriptors and CWMs occurred in May, August and September ( $p = 0.001, 0.048$  and  $0.011$  respectively), and explained 33.7% of



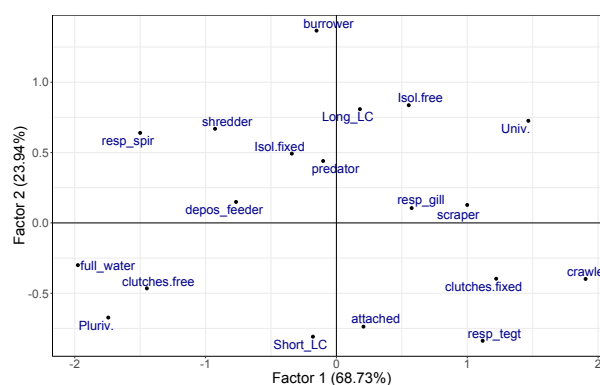
variation. The analysis of the interstructure revealed that July 11 and July 27 contributed the least to the compromise (contributions to the first eigenvalue of the compromise = 0.68, 0.58, 0.26, 0.50, 0.67 and 0.73 for May, June, July 11, July 27, August and September), meaning that the co-structure between the pair of environmental descriptors and species distribution tables was weaker at these two dates.

*Compromise* - Axes 1 and 2 of the compromise were clearly dominant in terms of explanatory power, explaining 68.7% and 23.9% of the total explained variance respectively. Axis 1 was primarily structured by the opposition between sites with high CPOM and high water temperature on the negative side (contributions = -1.05 and -1.74, respectively) and sites with high substrate structural diversity, high flooding frequency and high D50 for substrate size on the positive side (contributions = 2.54, 1.93 and 1.91, respectively). Axis 2 was largely structured by water temperature, nitrate concentration and CPOM biomass (contributions = -1.56, 1.44 and 1.08 respectively, Figure 11). The co-structure between environmental descriptors and species abundances was composed of two components, although the first one explained the majority of variation in CWMs: the first component represents the opposition between habitats that are frequently flooded, tend to have large and diverse substrate composition and also to be larger and better oxygenated, with sites that are less regularly flooded, with finer and more homogeneous substrate and higher CPOM biomass and water temperature. The second component may represent another environmental gradient within the floodplain: the opposition between habitats located along the true right bank of the floodplain at its downstream end which appear to exhibit a specific water type with elevated nitrate concentration, and the other habitats. The high concentration of nitrate in this part of the floodplain likely results from groundwater discharge from the adjacent alluvial terrace, as suggested by the presence of springs along that bank.

The analysis of CWM scores on the compromise suggested that the first environmental gradient affected the distribution of CWMs most strongly (Figure 12). For instance, the habitats on the positive side of the gradient (high flooding frequency, coarse heterogeneous substrate, high DO) had greater abundances of univoltine taxa which lay cemented/fixed egg clutches. These taxa were also primarily scrapers and with crawling as a primary mode of locomotion. On the other side of the gradient, taxa were primarily plurivoltine and lay free (non-attached) egg clutches. These taxa were primarily shredders, using a spiracle for breathing and with full water swimming as a primary mode of locomotion.



**Figure 11.** Graphical representation of the compromise produced by the STATICO analysis, with environmental descriptors coordinates.



**Figure 12.** Graphical representation of the compromise produced by the STATICO analysis, with species coordinates. Abbreviations for the trait categories are provided in Table 1.

*Community specialization* – The community specialization index averaged 0.30. It decreased from 0.312 in May to 0.307 in June, then increased to 0.314 in early July before steadily decreasing until September (0.304 in late July, 0.293 in August and 0.289 in September). Community specialization was significantly negatively affected by PC1, with communities more functionally homogeneous in habitats with higher HC ( $p = 0.015$ ,  $R^2_m = 0.26$ ).

## Discussion

Understanding the temporal variation in processes influencing metacommunity structure is essential to conserve the biodiversity and ecosystem functions in highly dynamic ecosystems, such as floodplains (Datry et al. 2016, Ruhi et al. 2017). Here we examined spatial and temporal patterns of macroinvertebrate diversity and specifically assessed how flooding affected environment-biota linkages. We also explored how metacommunity organization varied in time for groups of macroinvertebrates with differing dispersal abilities. We found that flooding homogenized environmental conditions within sub-sections of the floodplain and increased beta diversity. This reflected the stochastic distribution of taxa after the flood as suggested by the weak environment-trait linkages. Importantly, we found that metacommunity organization varied in time, with greater SS at later stages of assembly for both aerial and aquatic dispersers. Immediately after the flood, ME dominated for aerial dispersers whereas aquatic dispersers were distributed randomly, this highlighted the fact that dispersal mode had a great effect on temporal changes in metacommunity organization.

### *The floodplain as a mosaic of habitats and biotic assemblages*

The main environmental gradient filtering species consisted of a gradient of HC, opposing frequently-flooded, well-oxygenated, cool habitats to warm habitats with low flooding frequencies, a fine and homogeneous substrate and low DO levels. Surprisingly, we found that betadiversity consisted mostly of a nestedness component although we were expecting turnover along the main environmental gradient (Tonkin et al. 2016). The differences in community specialization along the main gradient, with functional homogenization of communities in rarely-inundated habitats, suggests that it might act as a stress gradient on communities (Smart et al. 2006, Devictor et al. 2008, Mondy and Usseglio-Polatera 2013). We did not find a

significant relationship between the main axis of environmental variation and species richness, despite a visible trend of higher species richness with higher HC. This absence of environmental control on species richness was surprising, also given that a previous study conducted in the same system had found a positive effect of substrate structural diversity on taxa richness (Chanut et al., in review). This could either be due to the fact that, once included in the PCA, the effect of the structural diversity index was not strong enough to drive a relationship between PC1 and taxa richness, or that by increasing stochasticity in species distributions, flooding had disrupted the relationship between environment and taxa richness. This also applied to the absence of environmental control on species evenness, whereas Chanut et al. (in review) found a negative relationship between resource level and community evenness.

The filtering of species traits along that main gradient was in line with our predictions: On the positive side of the gradient, the selected set of traits likely conferred a greater ability to live in frequently flooded habitats, with crawling as a primary locomotion mode and eggs laid as fixed clutches to resist high flows. The species found on the negative side of the gradient exhibited traits more associated with life in lentic habitats: full water swimming as a locomotion mode, respiration with a spiracle and eggs laid as free clutches. Surprisingly, univoltinism was more common in frequently disturbed, rather “lotic” habitats, where plurivoltinism would instead seem to be advantageous (Townsend and Hildrew 1994, Sheldon et al. 2010). But a similar pattern was found in other floodplain systems, with short-lived, plurivoltine species dominating in more isolated habitats, where they can make use of the habitat between periods of intense abiotic stress during long disconnection periods (Sheldon et al. 2010, Gallardo et al. 2013). Overall, we showed that the gradient of HC constrained structural and functional aspects of communities, yet flooding is known to greatly affect both environmental conditions and biotic assemblages.

#### *Temporal variability in environment-biota relationships*

We found that local environmental conditions were significantly more heterogeneous among sites in June than in May and early July, suggesting that flooding caused this divergence, which contradicts our hypothesis  $H_1$  and previous findings (see Thomaz et al. 2007). It is likely that during this particular flood, parafluvial habitats were not all affected in a similar manner. For instance, it is known that different floodplain areas experience varying flow velocities and therefore varying levels of hydraulic shear stress for a particular discharge, owing to differences in slope, sinuosity or location within the geomorphological setting (Bornette and Amoros 1996, Amoros and Bornette 2002).

Interestingly and contrary to  $H_1$  and our predictions, beta diversity also increased immediately after the flood. This suggests that flooding caused local communities to diverge structurally, which is also in opposition with previous findings and the general view that flooding homogenizes communities (Gomes et al. 2012, Bozelli et al. 2015 in Dittrich). But the divergence in community structures after the flood was not due to changes in the local environmental conditions, because the environmental control on community structure was low and trait-environment linkages were weak in June. This low environmental control related to flooding is in accordance with the theory that floods homogenize communities, but in opposition with previous studies in floodplains which showed that environmental control increased during high flows (Dias et al. 2016, Fernandes et al. 2014). In these two studies, Species Sorting dominated during inundation periods because aquatic species were released

from dispersal limitation and could track environmental variation. In the Maggia system, floods are typically short (duration <1 day) and act rather as disturbance than connectivity events, and it is unlikely that aquatic species then have time to track environmental conditions. This explains why our results of reduced environmental control immediately after flooding are more in line with the findings of Sarremejane et al. (2017b) who conducted their study in highly dynamic systems. Beta diversity did not decrease between June and early July like environmental conditions did, instead it remained relatively constant and decreased markedly only in August. This shows that communities may have conserved the structure they had acquired after the flood, and the convergence in community structures in August may reflect a strong environmental control or simply natural temporal patterns. Indeed, most of the generally more sensitive EPT taxa should have emerged at this stage, which could explain the decrease in beta diversity. Although the strong environmental control in the variance partitioning and the tight trait-environment linkages in August tend to suggest that species sorting is strong at that date.

### *Temporal changes in metacommunity organization differ with dispersal ability*

We found that SS was overall the dominant process acting on metacommunity organization, although ME may have occurred in May, June and on July 27, this was broadly in line with our predictions. The dominance of SS was reflected in the high environmental control, especially in May and August once the post-flood recolonization had slowed. Similarly, the minor spatial effects in May, June and July 27 are a sign that ME could have occurred. Interestingly, a large part of spatial effects in June were shared with the environment, this shows that environmental conditions were spatially structured after the flood and suggests that flooding had homogenized conditions within specific areas of the floodplain (Chaparro et al. 2018). This somewhat rectifies the first observation that flooding caused environmental conditions to diverge, in fact flooding may have homogenized conditions but only within particular areas of the floodplain. A spatial signal could describe either ME or DL (Heino et al. 2015), but following Tonkin et al. (2016), we argue that the small spatial scale, the absence of dispersal barriers, and the lower beta diversity than expected by chance strongly point at ME as a process homogenizing local communities. Overall, our findings that SS dominate as a structuring process and ME occur to a minor extent, are in line with the general patterns that aquatic communities tend to be primarily structured by local environment (Vanschoenwinkel et al. 2007, Waterkeyn et al. 2008, Göthe et al. 2013, Heino et al. 2015). Contrasting patterns emerged when taxa were separated according to their dispersal mode (likely a proxy for dispersal ability, given that aerial dispersers may disperse farther than swimmers).

For aquatic dispersers, in line with our predictions, SS dominated as a structuring process, especially in May and August. This was reflected in the strong environmental signal at these dates, although this signal was spatially structured in June and also shared with connectivity on July 27. For aerial dispersers, we found that SS and ME co-dominated, with SS occurring in May, late July and August, and ME (through the level of landscape connectivity) dominating after the flood in June and early July. This was highlighted by the relatively strong control of landscape connectivity after the flood in June and on July 11 and the comparatively weaker environmental control in May, July 27 and August. Overall, these findings supported our hypothesis H<sub>2</sub>.

Studies investigating the effects of dispersal ability on freshwater metacommunity structures have reported contrasting findings. For instance, Tonkin et al. (2016) and Thompson and Townsend (2006) both found that environmental control was stronger for aquatic and weak dispersers, whereas stronger dispersers were more affected by spatial distances. For Tonkin et al. (2016), the spatial control on aerial dispersers was an indicator of ME occurring at the small spatial scale of the study. On the contrary, Grönroos et al. (2013) found that environmental control was stronger for aerial active invertebrate dispersers in large-scale, complex river networks; Rodil et al. (2017) also found stronger environmental control for active macroinvertebrate dispersers than for passive ones, in a highly connected beach system. They attributed this environment control to the greater ability of aerial dispersers to track environmental variation. Here we propose that the balance between SS and ME may indeed vary with dispersal ability, connectivity and spatial scale, but also and especially with the assembly stage the metacommunity is at. Specifically, we showed that when no disturbance had recently occurred and the metacommunity was likely close to a stable state with less intense colonization, then SS dominated, irrespective of the dispersal mode of species. But when local communities were still re-assembling following disturbance, ME became the main structuring factor for taxa able to fly and disperse actively, and this not occurring for aquatic dispersers because they were unable to recolonize overland from other floodplain habitats. Instead their distributions were largely stochastic after the flood (in June and early July), and very moderate SS occurred along the then spatially structured environmental gradient.

As a whole, study shows that the balance between the processes structuring metacommunities in highly dynamic ecosystems vary with local environmental conditions, the degree of landscape connectivity and the dispersal ability of species, but also importantly with the stage of assembly following a disturbance. Several studies highlighted that metacommunity organization changes in time, primarily as a response to changes in connectivity levels. Here we reinforce that idea and add that considering temporal changes in metacommunity organization following disturbance is key to understanding environment-biota relationships in spatially complex, dynamic ecosystems. We suggest that future research could focus on characterizing the relationships between disturbance attributes (e.g. magnitude, frequency) and temporal shifts in metacommunity organization. Finally, our research implies that managers should focus on preserving flow variability in order to maintain habitat diversity and allow both strong dispersers and strong competitors to successively develop within the floodplain. But managers should also consider the degree of hydrological and landscape connectivity with respect to flooding frequency, in order to ensure that dispersal rates allow for recolonization between flood events.

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## References

- Amoros, C. and Bornette, G. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology* 47: 761-776.
- Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. – *Global Ecol. Biogeogr.* 19: 134–143.
- Bevenger G.S., and King RM. 1995. A pebble count procedure for assessing watershed cumulative effects. RM-RP-319. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO.; 17.
- Borcard, D., and Legendre, P. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling* 153: 51-68.
- Borcard, D., Legendre, P., Avois-Jacquet, C., and Tuomisto, H. 2004. Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85: 1826-1832.
- Bornette, G., and Amoros, C. 1996. Disturbance regime and vegetation dynamics: role of floods in riverine wetlands. *Journal of vegetation science*, 7:615-622,
- Boulton, A. J., Datry, T., Kasahara, M., and Stanford, J. A. 2008. Ecology and management of the hyporheic zone: stream–groundwater interactions of running waters and their floodplains. *Freshwater Science* 29: 26-40
- Bozelli R.L., Thomaz S.M., Padial A.A., Lopes P.M. & Bini L.M. (2015) Floods decrease zooplankton beta diversity and environmental heterogeneity in an Amazonian floodplain system. *Hydrobiologia*, 753, 233–241.
- Brown, B. L. and Swan, C. M. 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. – *J. Anim. Ecol.* 79: 571–580.
- Brunke, M., Hoehn, E., and Gonser, T. 2003. Patchiness of River–Groundwater Interactions within Two Floodplain Landscapes and Diversity of Aquatic Invertebrate Communities. *Ecosystems* 6: 707-722.
- Burnett, M. R., August, P. V., Brown, J. H., , and Killingbeck, K. T. 1998. The Influence of geomorphological heterogeneity on biodiversity: a patch-scale perspective. *Conservation Biology*, 12: 363-370.
- Cadotte, M. W. 2007. Competition-colonization tradeoffs and disturbance effects at multiple scales. *Ecology* 88:823- 829.
- Canedo-Arguelles, M. et al. 2015. Dispersal strength determines meta-community structure in a dendritic riverine network. – *J. Biogeogr.* 42: 778–790.
- Capderrey, C., Datry T., Foulquier, A., Claret, C., and Malard, F. 2013. Invertebrate distribution across nested geomorphic features in braided-river landscapes. *Freshwater Science* 32: 1188–1204.
- Cellot, B., Dole-Olivier, M. J., Bornette, G. and Pautou, G. 1994. Temporal and spatial environmental variability in the Upper Rhône River and its floodplain. *Freshwater Biology*, 31: 311-325
- Chanut, P., Datry, T., and Robinson, C. T. in review. Direct and indirect effects of flood regime on macroinvertebrate assemblages in a floodplain riverscape
- Chaparro G, Horváth Z, O'Farrell I, Ptacnik R, Hein T. 2018. Plankton metacommunities in floodplain wetlands under contrasting hydrological conditions. *Freshwater Biol.* 63:380–391.

- Cottenie, K. 2005. Integrating environment and spatial processes in ecological community dynamics. *Ecology Letters* 8:1175-1182.
- Datry, T., Bonada, N., and Heino, J. 2016a. Towards understanding the organization of metacommunities in highly dynamic ecological systems. *Oikos*, 125: 149-159.
- De Campos, R., de Oliveira da Conceição, E., Martens, K, and Higuti, J. 2019. Extreme drought periods can change spatial effects on periphytic ostracod metacommunities in river-floodplain ecosystems. *Hydrobiologia* 828: 369-381
- Devercelli, M., Scarabotti, P., Mayora, G., Schneider, B., and Giri, Federico. 2016. Unravelling the role of determinism and stochasticity in structuring the phytoplanktonic metacommunity of the Paraná River floodplain. *Hydrobiologia* 764:139-156.
- Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S. and Mouquet, N. .2010. Defining and measuring ecological specialization. *Journal of Applied Ecology*, 47: 15-25
- Dias, J.D., Simões, N.R., Meerhoff, M., Lansac-Tôha, F. A., Machado Velho, L. F., and Bonecker, C. C. 2016. Hydrological dynamics drives zooplankton metacommunity structure in a Neotropical floodplain. *Hydrobiologia* 781: 109-125
- Dolédéc, S. and Chessel, D. 1994. Co-inertia analysis: an alternative method for studying species–environment relationships. *Freshwater Biology*. 31: 277-294
- Faeh, R., Mueller, R., Rousselot, P., Veprek, R., Vetsch, D. and Volz, C. 2010. "BASEMENT - Basic Simulation Environment for Computation of Environmental Flow and Natural Hazard Simulation." Software Manual. VAW, ETH Zurich ([www.basement.ethz.ch](http://www.basement.ethz.ch)).
- Fairchild, G. W., Faulds, A. M., and Matta, J. F. 2000. Beetle assemblages in ponds: effects of habitat and site age. *Freshwater Biology* 44: 523-534.
- Fernandes, I. M., Henriques-Silva, R., Penha, J., Zuanon, J., & Peres-Neto, P. R. 2014. Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities. *Ecography* 37(5): 464-475.
- Gallardo, B., Doledec, S., Paillex, A., Arscott, D. B., Sgeldon, F., Zilli, F., Mérigoux, S., Castella, E., and Comin, F. A. 2014. Response of benthic macroinvertebrates to gradients in hydrological connectivity: a comparison of temperate, subtropical, Mediterranean and semiarid river floodplains. *Freshwater Biology* 59: 630-648.
- Gallardo, B., Garcia, M., Cabezas, A., Gonzalez, E., Gonzalez, M., Ciancarelli, C., and Comin, F. A. 2008. Macroinvertebrate patterns along environmental gradients and hydrological connectivity within a regulated river-floodplain. *Aquatic Sciences* 70: 248-258
- Gomes L.C., Bulla C.K., Agostinho A.A., Vasconcelos L.P. & Miranda L.E. 2012. Fish assemblage dynamics in a Neotropical floodplain relative to aquatic macrophytes and the homogenizing effect of a flood pulse. *Hydrobiologia*, 685, 97–107.
- Göthe, E. et al. 2013a. The influence of environmental, biotic and spatial factors on diatom metacommunity structure in Swedish headwater streams. – *PLoS ONE* 8: e72237.
- Grönroos, M. et al. 2013. Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context. – *Ecol. Evol.* 3: 4473–4487.
- Heino, J., Melo, A. S., Siquiera, T., Soininen, J., Valanko, S., and Bini, L. M. 2015. Metacommunity organisation, spatial extent, and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology* 60: 845-869.

- Holyoak, M., Leibold, M. A., Mouquet, N. M., Holt, R. D., and Hoopes, M. F. 2005. Metacommunities - A framework for large-scale community ecology. - *Metacommunities: Spatial Dynamics and Ecological Communities*: 1–31.
- Kuhn, N., and R. Amiet 1988. Bundesinventar der Auengebiete von Nationaler Bedeutung, Eidg. Dep. Inners, Bundesamt fuer For. und Landschaftschutz, Abt. Natur und Heimatschutz, Bern, Switzerland.
- Laliberté, E., and P. Legendre 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299-305
- Larned, S. T., & Datry, T. 2013. Flow variability and longitudinal patterns in parafluvial water chemistry, aquatic invertebrates and microbial activity. *Freshwater Biology* 58: 2126-2143.
- Leibold, M., A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J., B., Law, R., Tilman, D., Loreau, M., and Gonzalez, A. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7: 601-613
- Lindström, E. S., and Lagenheder, S. 2012. Local and regional factors influencing bacterial community assembly. *Environmental Microbiology Reports*, 4:1-9.
- Lowell, J. L., Gordon, N., Engstrom, D., Stanford, J. A., Holben, W. E., and Gannon, J. E. 2009. Habitat heterogeneity and associated microbial community structure in a small-scale floodplain hyporheic flow path. *Microbial Ecology* 58: 611-620.
- Malard, F., Tockner, K. and Ward J. V. 1999. Shifting dominance of subcatchment water sources and flow paths in a glacial floodplain, Val Roseg, Switzerland. *Arctic, Antarctic, and Alpine Research* 31: 135-150.
- Merritt R.W., Benbow M.E. & Hudson P.L. 2002. Wetland macroinvertebrates of Prentiss Bay, Lake Huron, Michigan: diversity and functional group composition. *Great Lakes Entomologist*, 35, 149–160.
- Molnar, P.; Favre, Natalie; Perona, Paolo; Burlando, Paolo; Ruf, Wolfgang. 2008. Floodplain forest dynamics in a hydrologically altered mountain river. *Peckiana - Staatliche Museum für Naturkunde Goerlitz*, Vol. 5
- Mondy, C. P. and Usseglio-Polatera, P. (2014), Using fuzzy-coded traits to elucidate the non-random role of anthropogenic stress in the functional homogenisation of invertebrate assemblages. *Freshw Biol*, 59: 584-600.
- Mondy, C. P. and Usseglio-Polatera, P. (2014), Using fuzzy-coded traits to elucidate the non-random role of anthropogenic stress in the functional homogenisation of invertebrate assemblages. *Freshw Biol*, 59: 584-600.
- Mondy, C. P. and Usseglio-Polatera, P. 2014. Using fuzzy-coded traits to elucidate the non-random role of anthropogenic stress in the functional homogenisation of invertebrate assemblages. *Freshw Biol*, 59: 584-600
- Mouquet, N., Munguia, P., Kneitel, J. M., and Miller, T. E. 2003. Community assembly time and the relationship between local and regional species richness. *Oikos* 103: 618-626.
- Opperman J. J., Luster, R., McKenney, B. A., Roberts, M., and Wrona Meadows, A. 2010. Ecologically functional floodplains: connectivity, flow regime and scale. *Journal of the American water resources association* 46: 211-226.



- Paillex, A., Doledec, S., Castella, E., and Mérioux, S. 2009. Large river floodplain restoration: predicting species richness and trait responses to the restoration of hydrological connectivity. *Journal of Applied Ecology* 46: 250-258.
- Paillex, A., Doledec, S., Castelly, E., Mérioux, S., and Aldridge, D. C. 2013. Functional diversity in a large river floodplain: anticipating the response of native and alien macroinvertebrates to the restoration of hydrological connectivity. *Journal of applied ecology* 50: 97-106.
- Perona, P., Camporeale, C., Perucca, E., Savina, M., Molnar, P., Burlando, P., and Ridolfi, L. 2009. Modelling river and riparian vegetation interactions and related importance for sustainable ecosystem management. *Aquat. Sci.* 71: 266 – 278
- Petsch, D. K., Pinha, G. D., and Michiyo Takeda, A. 2016. Dispersal mode and flooding regime as drivers of benthic metacommunity structure in a Neotropical floodplain. *Hydrobiologia* 788:31-141
- Pfamatter, S. and P. Zanetta. 2003. Hydrogologie de la plaine alluviale du valmaggia entre bignasco et giomaglio (Tessin). Master\_s thesis, Universitt Lausanne.
- Resh, V. H., Hildrew, A. G., Statzner, B., and TOWNSEND, C. R. 1994. Theoretical habitat templates, species traits, and species richness – a synthesis of long-term ecological research on the upper Rhône River in the context of currently developed ecological theory. *Freshwater Biology* 31:539–554.
- Rodil IF, Lucena-Moya P, Jokinen H, Ollus V, Wennhage H, et al. (2017) The role of dispersal mode and habitat specialization for metacommunity structure of shallow beach invertebrates. *PLOS ONE* 12(2): e0172160.
- Ruhí, A., Datry, T. and Sabo, J. L. 2017. Interpreting beta-diversity components over time to conserve metacommunities in highly dynamic ecosystems. *Conservation Biology*, 31: 1459-1468. doi:10.1111/cobi.12906
- Sarremejane R, Cañedo-Argüelles M, Prat N, Mykrä H, Muotka T, and Bonada N. 2017b. Do metacommunities vary through time? Intermittent rivers as model systems. *Journal of Biogeography* 44: 2752–2763.
- Sarremejane R, Mykrä H, Bonada N, Aroviita J, Muotka T. 2017a. Habitat connectivity and dispersal ability drive the assembly mechanisms of macroinvertebrate communities in river networks. *Freshwater Biol.* 2017a;62:1073–1082.
- Sheldon F., Bunn S.E., Hughes J.M., Arthington A.H., Balcombe S.R., and Fellows C.S. .2010. Ecological roles and threats to aquatic refugia in arid landscapes: dryland river waterholes. *Marine and Freshwater Research*, 61, 885–895.
- Simier, M., Blanc L., Pellegrin, F., and Nandris, D. 1999. Approche simultanée de K couples de tableaux: application à l'étude des relations pathologie végétale – environnement *Revue de statistique appliquée*, 47 : 31-46.
- Smart, S. M., Thompson, K., Marrs, R. H., Le Duc, M. G., Maskell, L. C., and Firbank, L. G. 2006. Biotic homogenization and changes in species diversity across human-modified ecosystems. *PROCEEDINGS OF THE ROYAL SOCIETY B*, 273, 2659–2665.
- Stanford J.A., Lorang M.S., and Hauer F.R. 2005. The shifting habitat mosaic of river ecosystems. *Verhandlungen des Internationalen Verein Limnologie*, 29, 123– 136
- Statzner B. & Bêche L.A. (2010) Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems? *Freshwater Biology*, 55, 80–119.

- Tachet H., Bournaud M., Richoux P., and Usseglio-Polatera P. 2010. Invertébrés d'eau douce - systématique, biologie, écologie. CNRS Editions, Paris. Accessed through [www.freshwaterecology.info](http://www.freshwaterecology.info) - the taxa and autecology database for freshwater organisms, version 7.0 accessed on 23.02.2018.
- Theobald D. M. et al. 2011. Assessing effects of land use on landscape connectivity: loss and fragmentation of western US forests. *Ecol. Appl.* 21: 2445 – 2458 .
- Thioulouse, J., Simier, M. and Chessel, D. 2004. Simultaneous analysis of a sequence of paired ecological tables. *Ecology*, 85: 272-283
- Thioulouse, J. and Chessel, D. 1987. Les analyses multitableaux en écologie factorielle. I. De la typologie d'état à la typologie de fonctionnement par l'analyse triadique. *Acta Oecol.-Oec. Gen.* 8: 463-480.
- Thioulouse, J., Chessel, D., Dolédec, S., and Olivier, J.M. 1997. ADE-4: a multivariate analysis and graphical display software. *Statistics and Computing*, 7: 75-83.
- Thomaz, S. M., Bini, L. M., and Bozelli, R. L. 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia* 579: 1-13
- Thompson, R., and Townsend, C. 2006. A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. *Journal of Animal Ecology* 75: 476-484
- Tockner, K., Malard, F., Burgherr, P., Robinson, C. T., Uehlinger, U., Zah, R., Ward, J. V. 1997. Physico-chemical characterization of channel types in a glacial floodplain ecosystem (Val Roseg, Switzerland). *Archiv für Hydrobiologie* 140: 433–463.
- Tonkin, J., Stoll, S., Jähnig, S., and Hase, P. 2016. Contrasting metacommunity structure and beta diversity in an aquatic-floodplain system. *Oikos* 125: 686-697.
- Townsend C., Dolédec S. and Scarsbrook M. 1997. Species traits in relation to temporal and spatial heterogeneity in streams: a test of habitat templet theory. *Freshwater Biology*, 37, 367–387.
- Townsend C.R. & Hildrew A.G. (1994) Species traits in relation to a habitat templet for river systems. *Freshwater Biology*, 31, 265–275.
- Vanschoenwinkel, B., De Vries, C., Seaman, M., and Brendonck, L. 2007. The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient. *Oikos* 116:1255-1266
- Waterkeyn, A., Grillas, P., Vanschoenwinkel, B., and Brendonck, L. 2008. Invertebrate community patterns in Mediterranean temporary wetlands along hydroperiod and salinity gradients. *Freshwater Biology* 53: 1808-1822.
- Wentworth, C., K. 1922. A scale grade and class terms for clastic sediments. *The Journal of Geology*, 30:377-392
- Winegardner, A. K., Jones, B. K., Ng, Y. S. Y., Siqueira, T., and Cotneie, K. 2012. The terminology of metacommunity ecology. *Trends in Ecology and Evolution* 73:253-254.

## Supporting information

**Table S1.** Wentworth substrate size classes

Size Code	Particle diameter range (mm)	Category
1	<0.062	silt/clay
2	0.062-0.125	very fine sand
3	0.125-0.25	fine sand
4	0.25-0.5	medium sand
5	0.5-1	coarse sand
6	1-2	coarse sand
7	2-4	fine gravel
8	4-5.7	medium gravel
9	5.7-8	medium gravel
10	8-11.3	coarse gravel
11	11.3-16	coarse gravel
12	16-22.6	small pebble
13	22.6-32	small pebble
14	32-45	large pebble
15	45-64	large pebble
16	64-90	small cobble
17	90-128	small cobble
18	128-180	large cobble
19	180-256	large cobble
20	256-362	boulder
21	362-512	boulder
22	512-1024	boulder
23	>1024	boulder
24	Bedrock	bedrock

**Table S2.** Results of the partitioning of beta diversity in overall beta diversity (Sorensen), and its turnover and nestedness components, for each date. The z-score result from the comparison between each observed metric and the null expectation, based on 10 000 simulations, using the R1 method to constrain null matrices. The p-values tested the significance of z-scores when the observed metric was greater than the null expectation.

<b>Date</b>	<b>Component</b>	<b>Observed</b>	<b>Null expectation</b>	<b>z - score</b>	<b>p.value</b>
<b>May</b>	Turnover	0.65	0.70	-3.75	-
	Nestedness	0.11	0.09	3.94	<i>0.001</i>
	Sorensen	0.76	0.79	-3.57	-
<b>June</b>	Turnover	0.63	0.69	-3.22	-
	Nestedness	0.14	0.11	3.31	<i>0.007</i>
	Sorensen	0.78	0.80	-3.09	-
<b>July 11th</b>	Turnover	0.54	0.62	-4.27	-
	Nestedness	0.18	0.14	4.43	<i>0.001</i>
	Sorensen	0.73	0.76	-4.02	-
<b>July 27th</b>	Turnover	0.66	0.71	-3.30	-
	Nestedness	0.12	0.09	3.45	<i>0.005</i>
	Sorensen	0.78	0.80	-3.12	-
<b>August</b>	Turnover	0.50	0.60	-5.44	-
	Nestedness	0.20	0.14	5.72	<i>&lt;0.001</i>
	Sorensen	0.70	0.74	-5.05	-
<b>September</b>	Turnover	0.61	0.69	-3.72	-
	Nestedness	0.14	0.10	3.92	<i>0.002</i>
	Sorensen	0.76	0.79	-3.48	-

## Chapter 4

# Flood disturbance affects food chain length in an alluvial river floodplain

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**Running Head:** Food chain length dynamics in an alluvial floodplain

**Abstract:** Characterizing food web responses to environmental factors could greatly improve our understanding of environment-biota relationships, and especially in floodplains where trophic interactions can be particularly important during phases of hydrological disconnection. The effects of floodplain hydrology and environmental attributes on structural aspects of biotic assemblages have been extensively studied, but responses at the functional level remain largely unknown. Here, we characterized a central aspect of food web architecture, the food chain length, as the maximum trophic position within 24 macroinvertebrate communities of parafluvial habitats in the Maggia river floodplain, in Switzerland. We investigated how the food chain length changed with different levels of habitat size, primary productivity and disturbance, the three factors potentially affecting food chain length in both theoretical and empirical studies. We found that food chain length was shorter in frequently flooded habitats and immediately after a flood. We also showed that trophic omnivory, where predators fed at lower trophic levels after flooding, and in more frequently flooded habitats, may explain these changes. These findings show that trophic omnivory may explain how predators resist disturbance and are maintained in highly dynamic landscapes. But more importantly, given that trophic omnivory should overall weaken trophic linkages, this suggests that it could be a key mechanism in sustaining biodiversity and in river floodplains.

**Keywords:** omnivory, stream invertebrates, pond, stable isotopes, flow regime, food webs

## Introduction

Riverine floodplains harbour high biodiversity, and deliver key ecosystem services to humans such as water cleansing and flood protection. Despite this, their ecological status is deteriorating rapidly worldwide and action is needed to protect these valuable ecosystems (Tockner and Stanford 2002, Tockner et al. 2010). In alluvial floodplains, floods create and maintain high habitat heterogeneity, resulting in ecological niches that sustain high levels of biodiversity (Arscott et al. 2002, Stanford et al. 2005, Datry et al. 2014). In fact, flood disturbance is a primary driver of floodplain ecological-biogeochemical functioning. Floods influence primary production by transferring nutrients from the main channel onto adjacent floodplains (Tockner et al. 1999, Tockner et al. 2000, Ahearn et al. 2006), enable organism dispersal among floodplain habitats (Paillex et al. 2007, Gallardo et al. 2008, Fernandes et al. 2014), and open new ecological niches for colonization by resetting communities to earlier successional stages (Townsend et al. 1997, Amoros and Bornette 2002, Thomaz et al. 2007). A number of studies have focused on understanding the environmental controls on community structure within alluvial floodplain ecosystems (reviewed in Amoros and Bornette 2002, Opperman et al. 2010), and have guided effective restoration efforts in many places. However, recent research shows that better knowledge of food web response to environmental drivers can improve our understanding of environment-biota relationships and assist species conservation in heterogeneous landscapes such as alluvial floodplains (Bellmore et al. 2013).

Food webs are a major focus in ecological research. Food webs describe the feeding links between species within a community and thus are important towards understanding biodiversity and ecosystem function response to environmental change (Thompson et al. 2012). Food chain length (FCL: maximum trophic position among all members of a food web) is a key attribute of food webs and is known to influence species diversity, community structure and stability (reviewed in Sabo et al. 2009), nutrient cycling, and contaminant concentrations in top predators (Cabana and Rasmussen 1994, Kidd et al. 1998, Sabo et al. 2009). Moreover, food webs tend to behave as linear food chains in resource-poor environments (Leibold et al. 1996, Holt and Polis 1997, Ward et al. 2015). FCL is an emergent property of food webs that incorporates different key processes such as the number of trophic levels and degree of trophic omnivory (Post 2002). Further, food web size largely results from a combination of basal resource diversity and FCL (Layman et al. 2007). In river floodplains with a low diversity of basal resources, for example, FCL variation may well capture changes in food web size and architecture and thus food web dynamics in general.

Ecosystem size, productivity, and disturbance level are three main features affecting food chain lengths (Sabo et al. 2009, Takimoto et al. 2013). The productivity hypothesis states that because much energy is lost at each trophic transfer (trophic efficiency usually ranges between 2% and 50%, Post et al. 2002), food chains will tend to be shorter in resource-limited ecosystems (Pimm 1982, Schoener 1989). The ecosystem size hypothesis posits that because larger habitats tend to be more environmentally diverse, they can accommodate more species and have longer food chains (May 1973, Cohen and Newman 1991, Post et al. 2000). Finally, the disturbance or dynamic stability hypothesis argues that long food chains are more vulnerable to disturbance and take longer to reassemble when disturbed, thus ecosystems with higher disturbance levels will have shorter food chains (Pimm and Lawton 1977, Pimm and Kitching 1987, May 2001). Each of these hypotheses has been supported to various degrees in experimental and natural systems, with FCL often positively affected by ecosystem productivity



and ecosystem size (reviewed in Takimoto et al. 2013). However, results still remain equivocal for the disturbance hypothesis. For instance, reviews by Post (2002) and Takimoto et al. (2013) found no evidence for an effect of disturbance on FCL, whilst Sabo et al. (2009) conducted a meta-analysis of determinants of FCL in freshwaters and found a negative effect of disturbance. One explanation for such inconsistency among these latter studies could be that drivers of FCL may interactive in a context-dependent manner (Post et al. 2002). For example, productivity levels can dampen the effect of disturbance in modelled food webs (Moore et al. 1993).

Food chains also can be shortened by the removal of a top predator or intermediate consumer, or by trophic omnivory of top predators feeding at lower trophic levels (Vander Zanden et al. 1999, Post and Takimoto 2007, Ruhi et al. 2016). The effect of trophic omnivory on food chain length has received considerable attention in recent years and several studies found that it explained food chain shortening in streams with high disturbance levels (McHugh et al. 2010, Ruhi et al. 2016). Omnivory is ubiquitous in freshwaters (Thompson et al. 2007, Thompson et al. 2012) and both theory and observations indicate that it is especially prevalent in ecosystems with high levels of disturbance and intermediate resource availability (Fagan 1997, France 2012).

Lastly, Warfe et al. (2013) suggested that analyzing mechanisms in parallel to FCL dynamics provides a framework for better understanding processes linking environmental drivers, community membership and food chain length. This additivity mechanism has received much attention in ecological research (Post et al. 2000) partly because understanding how top predators are maintained has far-reaching consequences on community assembly (McPeck 1998, Chase et al. 2002, Chase et al. 2009), nutrient cycling (Schmitz et al. 2010), and carbon storage (Atwood et al. 2013, Atwood et al. 2015). For example, Townsend et al. (1998) examined insertion mechanisms and found that insertion of feeding links increased FCL in more productive New Zealand streams.

Alluvial river floodplains are ideal ecosystems for studying the effects of environmental heterogeneity on biota (Tockner et al. 2010). In addition, examining food web structure across floodplain habitats could bridge the gap between classic small-scale food web studies and landscape ecology, thus providing a framework for understanding which food web attributes are important for sustaining species within heterogeneous landscapes (Winemiller 2005, Bellmore et al. 2013). Further, trophic interactions can play a particularly important role in structuring communities in floodplains, especially during phases of hydrological disconnection (Townsend et al. 1997, Fairchild et al. 2000, Mouquet et al. 2003, Cadotte 2007, Chanut et al. 2018 in review). Floodplains are often described as dynamic habitat mosaics with differing levels of disturbance, productivity, sizes and local environmental conditions (Amoros and Bornette 2002, Karaus 2005, Stanford et al. 2005, Whited et al. 2007). Altogether, alluvial floodplains are particularly suitable for examining the effects of habitat productivity, size and disturbance regime on FCL, reinforcing the call for food web studies in these systems.

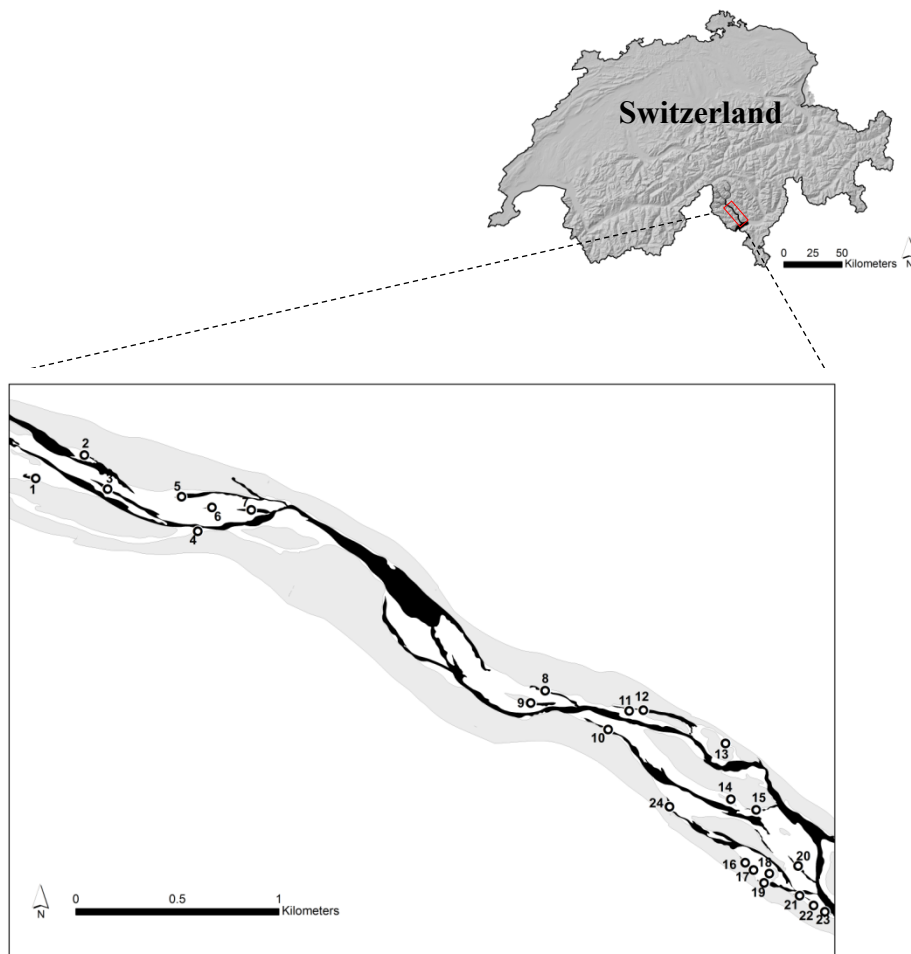
In the present study, we examined how habitat size, productivity and disturbance regime affect FCL in aquatic parafluvial habitats of an alluvial floodplain. We explored mechanisms (species addition/insertion, trophic omnivory) most likely explaining changes in FCL along measured environmental gradients. In our chosen study system, flow regulation has altered the seasonality of the flow regime and the interval time of floods is now largely uncorrelated to their magnitude (Perona et al. 2009). Consequently, environmental conditions largely differ from those under a natural flow regime to which local species are adapted (Lytle et al. 2004),

and floods likely act as disturbance to local communities as well as other properties of alluvial floodplains. We therefore hypothesized that flood disturbance would be the main force constraining FCL ( $H_1$ ). We also expected that species richness and community membership would be altered (reset) immediately after a flood, causing FCL to be shorter ( $H_2$ ). Lastly, following the dynamics stability hypothesis, we expected that frequently flooded habitats would have shorter food chains than less frequently flooded habitats ( $H_3$ ).

## Methods

### Study area

The Maggia River is located in the south-eastern part of the Swiss Alps, flowing southward into Lake Maggiore (Figure 1). It has one of the few remaining near-natural floodplains in Switzerland, being a site of national importance (Kuhn and Amiet 1988). Its catchment covers 930 km<sup>2</sup> with elevations ranging from 200 to 3300 m a.s.l. Owing to the presence of two glaciers in the headwaters and snowfall precipitation in winter, the hydrological regime is classified as glacio-nival. The flow regime of the river was substantially modified following the construction of a complex hydropower scheme in the headwaters in 1953 (Pfamatter and Zanetta 2003, Molnar et al. 2008). The original high flows during snowmelt were replaced by essentially constant flows (minimum flow requirements  $\sim 1.5$  m<sup>3</sup>/s) with occasional flood peaks and with no correlation between flood magnitude and return period (Molnar et al. 2008, Perona et al. 2009). The alluvial floodplain used in this study was located in the middle of the valley; it is about 7-km long and nearly 2-km wide in some sections. Because of fairly low storage by the hydropower scheme and high lateral hillslope runoff during major rain events, larger flood peaks still occur but not lesser magnitude floods  $<10$  m<sup>3</sup>/s. The combination of high flows and abundant bedload sediment (mean diameter of stones = 120 mm) maintains a heterogeneous floodplain mosaic. Within the floodplain, single-thread sections alternate with braided reaches where various types of parafluvial habitats occur: ponds, connected and disconnected side arms, and backwaters. For this study, we selected 24 permanently-wetted parafluvial habitats, including permanent ponds, disconnected side arms, and side arms connected at their downstream end to the main channel.



**Figure 1.** Map of Switzerland showing the location of the Maggia River floodplain and the parafluvial habitats sampled.

#### *Field sampling & laboratory analysis*

Samples were collected in February, August and October 2016. Of the initial 24 sites, we discarded sites where the collected invertebrate biomass did not allow accurate isotope measures (see below), retaining 17 sites from the February survey, 12 sites in August, and 20 sites in October. There were no consistent environmental or structural differences between the sites that were discarded and those that were retained. We measured habitat size as the surface area of each habitat using drone imagery and GIS. We used areas rather than volume because the invertebrate taxa collected were all benthic and therefore the available habitat is better captured by area than volume. Surface biofilms (periphyton) were measured by randomly collecting 5 stones (cobble-size) within each habitat. The biofilm was removed from each stone by scrubbing with a wire brush into a plastic container with 100 mL distilled water, and the scrubbed area measured (after Uehlinger 1991). The biofilm suspension was filtered through a glass fiber filter (0.45  $\mu\text{m}$ , Whatman GFF) and stored on ice in the dark. Chlorophyll-a extraction was conducted by incubating each half-filter in 6 mL 90% ethanol at 70°C for 10 minutes. Chlorophyll-a ( $\mu\text{g /L}$ ) was then determined using standard spectrophotometry (Hitachi 2000) following methods in Meyns et al. (1994). The other half of each filter was dried at 60°C for 24h, weighed, then combusted at 450°C for 6h and reweighed for estimates of particulate organic matter biomass as AFDM. The same procedure was repeated for 3 stone

replicates per site for stable isotope analysis and the filters with biofilms were preserved frozen (-25°C).

Benthic macroinvertebrates were collected in a semi-quantitative manner ( $n = 5$ , each site and date) using a kick-net (250- $\mu\text{m}$  mesh) following standard methods described in Stark et al. (2001) and immediately stored on ice. Macroinvertebrates were kept alive overnight, this is supposed to enable gut contents to be flushed and therefore not interfere with the isotopic signatures of invertebrate tissues. Macroinvertebrate samples were preserved frozen at -25°C until analysis. Particulate organic matter (POM) was collected at 3 locations within each habitat using a Hess sampler (250- $\mu\text{m}$  mesh, 0.04  $\text{m}^2$  area) by disturbing the substrate to a depth of ~10 cm. The collected POM was preserved frozen at -25°C. Once in the laboratory, POM was thawed, a subsample then dried at 60°C for 24h, weighed, combusted at 450°C for 6h and reweighed for estimates of biomass as AFDM. Potential basal resources also were collected at each site for isotope analysis: leaves and riparian plants were collected from 5 locations within each habitat and stored on ice before being preserved frozen (-25°C).

Macroinvertebrate samples were thawed in the laboratory, and individuals hand-picked and identified to the lowest possible taxonomic level using Tachet et al. (2010). Invertebrates were assigned as consumers or predators following Tachet et al. (2010).

Organic matter samples (biofilm and POM from above) were thawed and rinsed with distilled water. Biofilms, POM and invertebrates were then freeze-dried for 24h in a Lyovac GT 2-E lyophilizer (STERIS GmbH, Hürth, Germany). Each invertebrate and organic matter sample was homogenized with a mortar and pestle and ca. 0.5-1.5mg of each placed into a tin cup. All samples were combusted in a Vario PYRO Cube elemental analyzer (elementar Analysensysteme GmbH, Langenselbold, Germany) connected to an IsoPrime isotope ratio mass spectrometer (GV Instruments Ltd., Wythenshawe, UK) for measurement of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Reference materials for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were provided by Biogeochemical Laboratories, Indiana University (NBS 19, L-SVEC, IAEA-N-1 and IAEA-N-2). Analytical precision was 0.01‰ for  $\delta^{13}\text{C}$  and 0.02 ‰ for  $\delta^{15}\text{N}$ .

### *Habitat characterization*

*Hydrological regime-* We developed a 2D hydrodynamic model for the floodplain that enabled us to calculate two key hydrological metrics for each habitat: flood frequency over the two years preceding a sampling event and recent disturbance history represented by the number of days elapsed since the last flood. For a detailed description of the model and its accuracy, see Chanut et al. 2018 (in review). The model was constructed using Basement software (Faeh et al. 2010, developed at ETH Zurich: <http://www.basement.ethz.ch/>), which solves depth-averaged shallow-water Saint-Venant equations to calculate water depth, current velocity and bottom shear stress for each element within the modelling domain. Because of the spatial complexity of groundwater-surface water interactions in this alluvial floodplain that cannot be accurately simulated under the current state of system characterization, we only used the model to derive thresholds of discharge at which a given habitat becomes inundated with surface water as well as local bottom shear stress. Our modelling approach consisted of running steady-state simulations for the range of flows corresponding to flood peaks that occurred between 13 March 2014 and the end of our study period on 28 October 2016. During this period, 45 identified flood events occurred with a maximum discharge of 570  $\text{m}^3/\text{s}$ . For each discharge simulation, the model produced a simulated water depth for each cell of the modelling domain

that was then overlapped with a map of our sampling sites to determine whether a particular habitat was flooded at a given discharge. We were then able to calculate a flood frequency for each habitat during the modelling period as well as the time elapsed since the last flood at each sampling campaign (February, August and October). During the modelling period, 45 floods occurred, with a minimum discharge of 20.1 m<sup>3</sup>/s, a maximum of 570 m<sup>3</sup>/s, and average of 141.2 m<sup>3</sup>/s and standard deviation 164.8.

#### *Data analysis*

*Isotopic niche indices* – We computed the trophic position of each predator *i* in site *j* as:

$$TP_{ij} = \lambda + (\delta^{15}N_{ij} - \delta^{15}N_{base,j})/\Delta$$

Where  $\delta^{15}N_{ij}$  is the  $\delta^{15}N$  value for the predator *i* in site *j*,  $\delta^{15}N_{base,j}$  is the lowest value for a consumer within site *j* (Table 1),  $\lambda$  is the trophic position of the primary consumer (i.e. 2) and  $\Delta$  is the mean fractionation factor of 2.2‰ (McCutchan et al. 2003). We chose to use the minimum consumer  $\delta^{15}N$  value at each site as a basal reference for our calculations, because isotopic signatures of primary consumers average the values of basal resources, which varied considerably among sites and dates (Jardine et al. 2014). We estimated FCL within each habitat as the maximum trophic position (MTP) occupied by a predator (Post et al. 2000, Ruhi et al. 2016, Table 2). Total food web size was calculated as the stable ellipse area corrected for sample size (SEAc), and all analyses including this metric were restricted to sites with at least 5 invertebrate taxa because SEAc calculations become uncertain when  $n < 5$  (Jackson et al. 2011).

**Table 1.** List of consumer taxa and proportions of habitats where they occupy the lowest trophic position.

<b>Taxa</b>	<b>Frequency</b>
Chironomidae	2.0 %
Corixidae	57.1 %
Elmidae	6.1 %
Ephemerella	2.0 %
Habrolepoides	2.0 %
Haliplidae	6.1 %
Heptagenidae	2.0 %
Hydropsyche	2.0 %
Hydroptilidae	6.1 %
Leuctridae	2.0 %
Tipulidae	12.2 %

**Table 2.** List of predatory taxa (according to Tachet 2010) and proportions of habitats where they occupy the maximum trophic position.

Taxa	Frequency
Athericidae	16.3 %
Chloroperlidae	10.2 %
Dytiscidae	4.1 %
Limoniidae	38.8 %
Perlidae	2.0 %
Rhyacophilidae	6.1 %

*Isotope mixing model analyses* – We used stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) mixing models to estimate the proportional contributions of different basal resources to invertebrate food webs within each habitat. We tested whether consumer isotope values could be suitable for use with mixing models using the Monte Carlo simulation of the possible range of isotopic mixing models developed by Smith et al. (2013). A total of 1500 iterations were performed with sources corrected by ranges for trophic enrichment factors (TEF): for  $\delta^{13}\text{C}$ ,  $0.4 \pm 0.3$ , and for  $\delta^{15}\text{N}$ ,  $2.2 \pm 0.3$  (Post 2002, McCutchan et al. 2003). Samples were excluded from further analysis when they fell outside the 95% confidence bounds indicating suitability for mixing model analysis (Smith et al. 2013, Philips et al. 2014). Next, we used the Bayesian mixing model SIAR (Parnell et al. 2010) to produce probability distributions of the contributions of basal resources to consumer isotope values. As filamentous algae were rarely found, the model was restricted to two basal resources (terrestrial plant litter and periphyton). We did not include prior information on diet proportions as there were only two sources in the mixing model (Fry 2013, Brett 2014). Models were run separately for each site and season (February, August, and October). Terrestrial plant and periphyton  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were set at averages and standard deviations for each season. Each model was set to run 500,000 times, with the first 50,000 iterations discarded. All models were created using the SIAR package in R 3.5.0 (R core team, 2018).

#### *Statistical analysis*

In order to test which of the three FCL control hypotheses was supported more, we constructed a global generalized linear mixed effect model (GLMM) including all potential drivers of FCL: biofilm standing crop ( $\text{g/m}^2$ ), particulate POM ( $\text{g/m}^2$ ), habitat surface area ( $\text{m}^2$ ), time since last flood (days), and flooding frequency (flood events/year). Because of the repeated-measures structure of our dataset, we used site ID as a random effect in all models to account for unmeasured site-specific effects and season as a fixed factor in each model to correct for seasonal effects. All GLMMs were constructed with the lme4 R package (Douglas et al. 2015). We then used a backward model selection procedure based on the Akaike Information Criterion (AICc), where model terms are sequentially removed until the most parsimonious model with the lowest AICc is found.

We also tested the relative importance of each of the three potential mechanisms driving FCL. For the insertion mechanism, we tested the relative effects of each of the potential FCL drivers on community composition of primary consumers (Ruhi et al. 2016). For this, we

constructed a distance-based redundancy analysis model using the Jaccard index (distance between sites based on species occurrences), incorporating all potential drivers of FCL. We then conducted a similar backward model selection procedure as for the controls of FCL with the fixed effect “season” being incorporated in all final models. The same procedure was repeated on the predator assemblage to test for addition mechanisms. We tested the effect of taxa richness on FCL using a GLMM with site ID as a random effect and season as a fixed effect. We examined the omnivory hypothesis by testing which of the potential drivers of FCL most affected the average trophic position of all predators at a site (Ruhi et al. 2016). Here, we used a similar GLMM and model selection procedure as for the FCL control with average trophic position of predators as the independent variable. Lastly, we tested whether organic matter availability (POM, biofilm) affected FCL when community-wide dietary proportions were primarily based on organic resources using a similar GLMM on median values of diet proportions (Macarelli et al. 2011). To test for an effect of productivity on FCL, we separated sites along the community-wide diet proportions at a 50% level cut-off; i.e., communities were primarily fueled either by biofilm or POM. We then tested whether the availability of each resource type (biofilm and POM) affected FCL in each category. Finally, we tested whether FCL was indeed a good representation for food web dynamics in this system by evaluating the correlation between FCL and trophic diversity (SEAc). Here, we report the marginal  $R^2$  for all GLMMs.

## Results

### *Environmental drivers overview*

Surface areas of parafluvial habitats ranged from 7.2 to 877.2 m<sup>2</sup> and productivity levels varied widely among habitats: POM ranged from 0.04 to 2.18 g/m<sup>2</sup> and biofilm standing crop from 0 to 14.2 g/m<sup>2</sup>. Discharge threshold values for habitat inundation ranged from 10 to 250 m<sup>3</sup>/s (mean = 49 m<sup>3</sup>/s, median = 35 m<sup>3</sup>/s, SD = 58 m<sup>3</sup>/s). Flood frequency for the different parafluvial habitats ranged from 0.52 to 18.04 floods per year (Table S3, Supporting Information). Time elapsed since the last flood varied greatly among habitats at each date, owing to the wide range of inundation thresholds (Table S3, Supporting Information). There was some level of covariation between some of these metrics, but none exceeded a Spearman Rank coefficient of 0.42 (Table S1, Supporting Information).

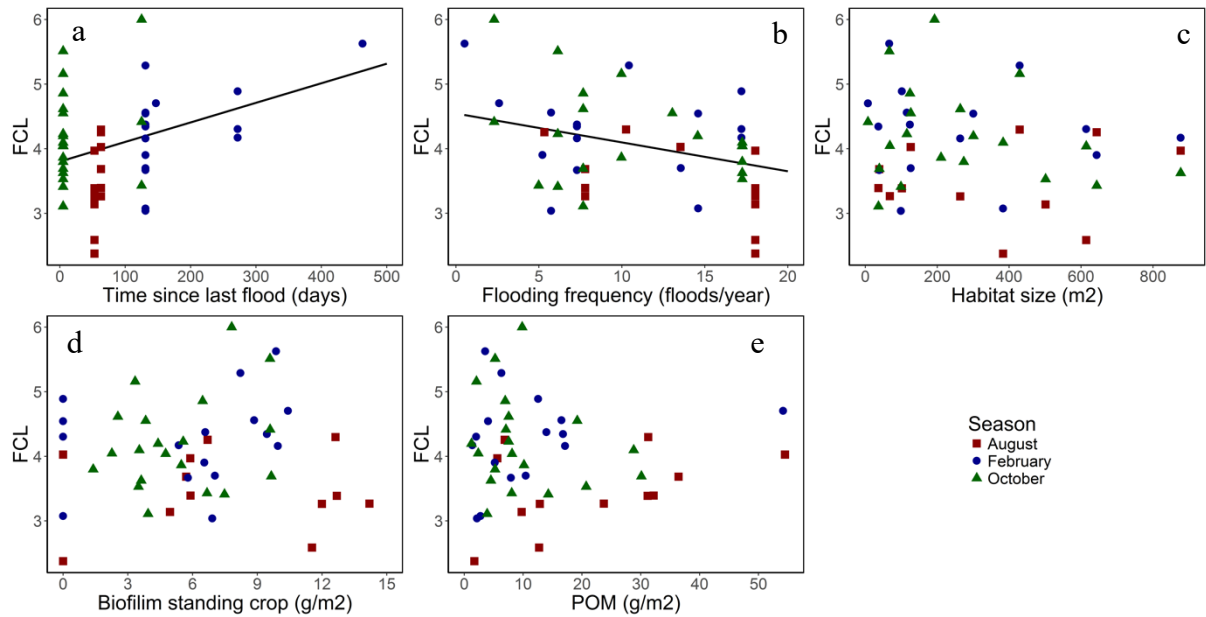
### *Food web overview*

A total of 40 invertebrate taxa were identified, of which 30 were primary consumers and 10 were predators (Table S2, Supporting Information). FCL ranged from 2.89 to 5.62 in February, from 2.37 to 4.29 in August and from 3.10 to 5.99 in October. Trophic diversity (SEAc) ranged from 2.24 to 43.38 (median = 12.94). The median values for the distribution of the proportion of diet composed of POM varied between 0.25 and 0.65 in February (median = 0.49), 0.20 and 0.57 in August (median = 0.44) and between 0.16 and 0.67 in October (median = 0.42).

### *Environmental controls on food chain length*

SEAc was positively correlated to FCL ( $p = 0.0002$ ,  $R^2 = 0.432$ ), suggesting that changes in the vertical dimension of the food web accounted to a large extent for variations in food web

size. The final model retained for FCL ( $AIC_c = 101.68$ ,  $R^2 = 0.376$ ) included a positive linear relationship between FCL and time since last flood ( $p = 0.047$ , Figure 2a) and a negative relationship with flooding frequency ( $p = 0.036$ , Figure 2b). The other terms in the initial global model were not retained in the model selection because FCL was not correlated to habitat size (Figure 2c), biofilm standing crop (Figure 2d), or biomass of POM (Figure 2e). When we separated food webs based on their community-wide dietary proportions, FCL was not correlated to biofilm standing crop (Figure 2d) for food webs with a community-wide dietary proportion composed of  $>0.5$  biofilm ( $p = 0.09$ ). Similarly, FCL was not correlated to POM biomass for food webs with a community-wide dietary proportion composed of  $>0.5$  POM ( $p = 0.51$ ).



**Figure 2.** Plots showing the effects of the time since last flood (a), flooding frequency (b) habitat size (c), biofilm standing crop (d) and POM (e) on FCL. Plots (a) and (b) also show the significant linear relationships calculated with GLMMs.

#### *Potential mechanisms driving changes in FCL*

The composition of primary consumer and predator assemblages was not affected by any measured FCL drivers (Table 3). FCL was not correlated to taxa richness ( $p = 0.254$ , Figure S1, Supporting Information). For the test of omnivory, the final model ( $AIC_c = 293.98$ ,  $R^2 = 0.315$ ) included positive relationships between the trophic position of predators and the time since last flood ( $p = 0.004$ , Figure S2b Supporting Information), POM ( $p = 0.014$ , Figure S2c Supporting Information) and a negative relationship with flooding frequency ( $p = 0.003$ , Figure S2a Supporting Information).



**Table 3.** Results of the backward model selection performed on the distance-based redundancy analysis model testing the effect of putative FCL drivers on the similarity of predator and consumer assemblages (based on Jaccard's distance).

Response	Driver	AICc	F	p	Proportion of variation explained
Predators	Habitat size	183.11	1.074	0.35	0.174
	POM	183.28	0.913	0.41	
	Biofilm	183.88	0.356	0.89	
	Time since last flood	184.02	0.226	0.97	
	Flooding frequency	184.09	0.154	0.98	
Consumers	Time since last flood	238.41	1.576	0.06	0.219
	Biofilm	238.43	1.559	0.08	
	Flooding frequency	238.5	1.485	0.11	
	POM	238.59	1.404	0.13	
	Habitat size	238.83	1.177	0.35	

## Discussion

In this study, hydrological disturbance negatively affected food chain length (FCL) in parafluvial habitats of an alluvial floodplain. Trophic omnivory where predators fed at lower trophic levels after flooding, and in more frequently flooded habitats, may explain these changes in FCL. This result shows that flooding can have minor direct effects on community composition and species richness but still cause substantial changes in food webs, which thus influences structural and functional properties of ecosystems. These results consequently have potentially important implications for species conservation in alluvial floodplains.

### *FCL is affected by hydrological disturbance in an alluvial floodplain*

Here we tested how ecosystem size, productivity, and disturbance regime affected FCL in an alluvial floodplain. The strong positive correlation between food web size (SEAc) and FCL showed that changes in FCL accounted for a large part of the variation in food web structure. This result confirmed that examining FCL dynamics in this system largely captured changes in food web structure among parafluvial habitats.

We found that only the dynamic stability hypothesis was supported by the data, in accordance with H<sub>1</sub>. Specifically, food chains were shorter after a flood and in frequently flooded habitats. To date, variations in FCL in natural systems have most often been attributed to gradients of productivity or ecosystem size, but the effect of disturbance remains equivocal and little documented (but see McHugh et al. 2010, Sabo et al. 2010, Ruhi et al. 2016). McHugh et al. (2010) and Ruhi et al. (2016) quantified disturbance as a combination of geomorphological metrics and hydrological variability and found that stream reaches with high disturbance levels had shorter food chains. Sabo et al. (2010) found that increased hydrologic variability reduced FCL in 36 North American rivers. Here we show that flood disturbance is the main driver behind FCL changes in an alluvial floodplain system. Although the effect of disturbance on FCL remains uncertain both in terrestrial and freshwater systems (Post et al. 2002, Takimoto et

al. 2013), our results are significant not only for the understanding of floodplain functioning, but also for our understanding of the drivers of FCL in general.

Parafluvial habitats in floodplains share characteristics of both ponds and streams, and the positive effect of habitat size on FCL in these systems has been well documented (Takimoto et al. 2013). In contrast, we found no support for this hypothesis. This finding may potentially be due to the range of habitat sizes in our floodplain, which may have been too narrow to have an effect on FCL. For instance, Tunney et al. (2012) showed that food chains were longer in larger lakes, where the top predators (pelagic fish in this case) primarily relied on pelagic resources, whereas in smaller lakes with a higher proportion of benthic littoral habitat, food chains were shorter and omnivory prevailed. The shallow depth (<1m) and overall small size of parafluvial habitats could not sustain a pelagic food web decoupled from benthic and littoral habitats, which could explain the absence of relationship between habitat size and FCL. Yet, fish are known to be present in the Maggia floodplain, and we cannot exclude that FCL response to habitat size may have differed if fish had been included in our calculations of FCL.

We found that the availability of organic resources did not affect FCL, even when we separated food webs according to respective community-wide dietary proportions. By doing so, we attempted to take into account that POM-fuelled food chains may be more sensitive to changes in POM availability and similarly those fuelled by biofilms. Post et al. (2002) pointed out that the positive effect of resource availability on FCL remains uncertain in natural ecosystems. By comparing the range of available resource stocks between studies that reported an effect and those that did not, the authors concluded that resource availability affects FCL only at extremely low resource levels (between 1 and 100 g C m<sup>-2</sup> y<sup>-1</sup>). This finding may explain why we found no effect of resource availability on FCL here. Further, biofilm standing crops were slightly negatively affected by flooding frequency in our system, suggesting that some of effects by organic resources on FCL may have been confounded.

In floodplain systems, Saigo et al. (2015) and Warfe et al. (2013) found little support for the three examined mechanisms tested in this study. These studies were completed in large river-floodplain systems where top predators were fish, and where long-lasting seasonal inundation periods enabled them to disperse between floodplain habitats, potentially dampening local controls on FCL (Saigo et al. 2015). In a sub-alpine alluvial floodplain like the Maggia system, floods are episodic, rarely lasting more than a day, and act as disturbance on aquatic ecosystem (Amoros and Bornette 2002, Opperman et al. 2010). This difference makes it difficult to directly compare our results with these two studies of FCL in floodplains, along with the fact that top predators in our study were limited to macroinvertebrates.

#### *Trophic omnivory from predators drive changes in FCL*

The fact that both flooding frequency and time since last flood affected FCL is a strong indication that both long-term flooding history and recent disturbance status affects FCL. Additionally, this result suggests that floods shorten food chains, and FCL remains short in habitats that are frequently flooded. Yet, flooding frequency and time since last flood had no effect on community composition of consumer and predator assemblages. This result suggests that because species occurrences were not related to drivers of FCL, neither insertion nor addition mechanisms were responsible for observed changes in FCL along flood disturbance gradients, thus rejecting H<sub>2</sub> (Ruhi et al. 2016). This finding was further supported by the lack of correlation between taxa richness and FCL, showing that shorter food chains did not include

significantly fewer species. Indeed, species occurrence and richness did not vary along the gradient of flooding frequency and time since last flood. Since FCL can only vary with insertion or deletion of species, or changes in trophic position of predators, this strongly suggests that trophic omnivory may be the mechanism driving changes in FCL in ponds of this floodplain. In support, we found that the average trophic position across all predatory taxa was negatively affected by flooding frequency and positively affected by the time since last flood, similarly to FCL.

These shifts in trophic position indicate that trophic omnivory by predators feeding at lower trophic levels occurs after flood disturbance or in ponds where flooding frequency is high. McHugh et al. (2010) and Ruhi et al. (2016) also found that both fish and invertebrate predators fed at lower trophic levels when the level of hydrological disturbance increased in streams. The fact that predator trophic position also increased with availability of POM, although it did not affect community membership, suggests that predators were able to feed at higher trophic levels in POM-rich habitats irrespective of their disturbance regime. However, this effect was not strong or consistent enough among predators to result in food chain lengthening in this study.

Omnivory is ubiquitous in freshwaters, and omnivores are more common in highly disturbed environments because they can shift their diet when resource availability varies (Fagan 1997). Empirical studies have shown that intermediate levels of trophic omnivory increase food web stability (Denno and Fagan 2003, Thompson et al. 2012), and may therefore be “selected for” in highly disturbed environments. Because feeding at lower trophic levels often entails feeding on lower-quality resources (France 2012), it is likely that predators only shift their diet under necessity. This necessity may arise when environmental constraints shift the biomass distribution in the food chain towards a top-heavy distribution, when predators first recolonize after a flood for instance (Ward et al. 2017). If predators cannot disperse in search of higher-quality resources (Warfe et al. 2013), omnivory may act as a stabilizing force because predators must resort to feeding lower down the food chain. This shift in feeding releases primary consumers higher up the food chain from strong predation (Diehl 2003, Diehl and Feissel 2001). In contrast, stronger trophic interactions may result in the loss of consumers when strong predation adds to environmental constraints (Wootton 2017).

We found no effect of flood disturbance on the occurrence of species, but it is likely that predators were “forced” to feed lower down the food chain because prey availability in higher trophic levels was lower after flooding and in frequently flooded habitats. In a previous study examining structural changes in invertebrate communities in this floodplain, Chanut et al. (2018, in review) found that flooding frequency and time since last flood affected the relative abundances of Coleoptera, Diptera and EPT taxa. The effect of flooding frequency suggests that frequent flooding does not allow for rapid development of resources higher up the food chain, irrespective of the time since last flood. We cannot entirely rule out the potential effect of biofilm resource availability on trophic omnivory because it was weakly negatively correlated to flooding frequency and thus effects may be confounded.

Moderate levels of omnivory can act as a stabilizing force on communities (Emmerson and Yearsley 2004, Gellner and McCann 2012, Thompson et al. 2012, Cross et al. 2013, Ward et al. 2017). Therefore, understanding conditions in which the stabilizing effect of omnivory arises is key to understanding the response of food webs and communities to environmental change (Kratina et al. 2012, Wootton 2017). It is well documented that restoring variable flow

regimes results in higher biodiversity in floodplains (Amoros and Bornette 2002, Opperman et al. 2010) because it maintains a dynamic habitat mosaic. We suggest that because predators feed on different resources depending on the disturbance regime, maintaining the spatial heterogeneity in disturbance within a floodplain can result in overall weaker trophic interactions between predators and consumers. This, in effect, could increase the stability of the food web at the floodplain scale (Bellmore et al. 2015). Additionally, by shifting their diets, omnivorous predators may enable depleted consumer populations to better recover from environmental disturbance (Singer and Bernays 2003, Abrams and Fung 2010, Wootton et al. 2017). We suggest that with spatially heterogeneous disturbance such as flooding, trophic omnivory causes the strength of trophic interactions between predators and consumers to vary among habitats, acting as spatial insurance (Loreau et al. 2003) where local populations of consumers are rescued from local extirpation by dispersal from other habitats where predatory pressure is diminished. Overall, maintaining the spatial mosaic of disturbance levels in floodplains thus results in greater gamma diversity. We suggest that examining trophic omnivory in floodplains and its effect as a stabilizing force both within habitats at the community level and also at the landscape scale would be useful towards conserving these complex, threatened ecosystems.

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## References

- Abrams, P. A., and Fung, S. R. 2010. The impact of adaptive defence on top-down and bottom-up effects in systems with intraguild predation. *Evolutionary Ecology Research*, 12, 307–325.
- Ahearn D. S., Viers, J. H., Mount, J. F. and Dahlgren, R. A. 2006. Priming the productivity pump: flood pulse driven trends in suspended algal biomass distribution across a restored floodplain. *Freshwater Biology*, 51: 1417-1433.
- Amoros, C., and Bornette, G. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology* 47: 761-776.
- Arscott, D. B., Tockner, K., Van der Nat, D., and Ward, J. V. 2002. Aquatic Habitat Dynamics along a Braided Alpine River Ecosystem (Tagliamento River, Northeast Italy). *Ecosystems* 5:802-814
- Atwood, T. B., Hammill, E., Greig, H. S., Kratina, P., Shurin, J. B., Srivastava, D. S., and Richardson, J. S. 2013. Predator-induced reduction of freshwater carbon dioxide emissions. *Nature Geoscience*, 6: 191-194
- Atwood, T. B., Connolly, R. M., Ritchie, E. G., Lovelock, C. E., Heithaus, M. R., Hays, G. C., fourqurean, J. W., and Macreadie P. I. 2015. Predators help protect carbon stocks in blue carbon ecosystems. *Nature Climate Change*. 5:1038-1045.
- Bellmore, J. R., Baxter, C. V., Martens, K. and Connolly, P. J. 2013. The floodplain food web mosaic: a study of its importance to salmon and steelhead with implications for their recovery. *Ecological Applications*, 23: 189-207. doi:10.1890/12-0806.
- Bellmore, J. R., Baxter, C. V. and Connolly, P. J. 2015. Spatial complexity reduces interaction strengths in the meta-food web of a river floodplain mosaic. *Ecology*, 96: 274-283. doi:10.1890/14-0733.1
- Bevenger G.S., and King RM. 1995. A pebble count procedure for assessing watershed cumulative effects. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO.; 17.
- Brett, M. T. 2014. Resource polygon geometry predicts Bayesian stable isotope mixing model bias. – *Mar. Ecol. Prog. Ser.* 514: 1–12.
- Brunke, M., Hoehn, E., and Gonser, T. 2003. Patchiness of River–Groundwater Interactions within Two Floodplain Landscapes and Diversity of Aquatic Invertebrate Communities. *Ecosystems* 6: 707-722.
- Burnett, M. R., August, P. V., Brown, J. H., and Killingbeck, K. T. 1998. The Influence of geomorphological heterogeneity on biodiversity: a patch-scale perspective. *Conservation Biology*, 12: 363-370.
- Cabana G, and Rasmussen, J.B. 1994. Modelling food chain structure and <sup>15</sup>N contaminant bioaccumulation using stable nitrogen isotopes. *Nature* 372: 255–257.
- Cadotte, M. W. 2007. Competition-colonization trade-offs and disturbance effects at multiple scales. *Ecology* 88:823- 829.
- Cellot, B., Dole-Olivier, M. J., Bornette, G. and Pautou, G. 1994. Temporal and spatial environmental variability in the Upper Rhône River and its floodplain. *Freshwater Biology*, 31: 311-325

- Chanut, P., Datry, T., and Robinson, C. T. 2018. Direct and indirect effects of flood regime on macroinvertebrate assemblages in a floodplain riverscape. Inreview
- Chase, J. M., and Leibold, M. A. 2002. Spatial scales dictate the productivity-biodiversity relationship. *Nature*, 416: 427-430.
- Chase, J. M., Biro, E. G., Ryberg, W. A. and Smith, K. G. 2009. Predators temper the relative importance of stochastic processes in the assembly of prey metacommunities. *Ecology Letters*, 12: 1210-1218. doi:10.1111/j.1461-0248.2009.01362.x
- Cohen J. E., and Newman C. M. 1991. Community area and food-chain length: <sup>[SEP]</sup>theoretical predictions. *American Naturalist*. 138: 1542–1554. <sup>[SEP]</sup>
- Cross, W. F., Baxter, C. V., Rosi-Marshall, E. J., Hall, R. O., Kennedy, T. A., Donner, K. C., ... Yard, M. D. 2013. Food-web dynamics in a large river discontinuum. *Ecological Monographs*, 83, 311–337.
- Datry, T., Corti, R., Belletti, B. and Piégay, H. 2014. Ground-dwelling arthropod communities across braided river landscape mosaics: a Mediterranean perspective. *Freshw Biol*, 59: 1308-1322.
- Denno, R. F., & Fagan, W. F. 2003. Might nitrogen limitation promote omnivory among carnivorous arthropods? *Ecology*, 84, 2522–2531.
- Diehl, S. 2003. The evolution and maintenance of omnivory: Dynamic constraints and the role of food quality. *Ecology*, 84, 2557–2567.
- Diehl, S., and Feissel, M. 2001. Intraguild prey suffer from enrichment of their resources: A microcosm experiment with ciliates. *Ecology*, 11, 2977–2983.
- Douglas Bates, Martin Maechler, Ben Bolker, Steve Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1-48. doi:10.18637/jss.v067.i01.
- Emmerson, M., & Yearsley, J. M. 2004. Weak interactions, omnivory and emergent food-web properties. *Proceedings of the Royal Society B: Biological Sciences*, 271, 397–405.
- Fagan, W. 1997. Omnivory as a stabilizing feature of natural communi- ties. *The American Naturalist*, 150, 554–567.
- Faeh, R., Mueller, R., Rousselot, P., Veprek, R., Vetsch, D. and Volz, C. 2010. "BASEMENT - Basic Simulation Environment for Computation of Environmental Flow and Natural Hazard Simulation." Software Manual. VAW, ETH Zurich (www.basement.ethz.ch).
- Fairchild, G. W., Faulds, A. M., and Matta, J. F. 2000. Beetle assemblages in ponds: effects of habitat and site age. *Freshwater Biology* 44: 523-534.
- Fernandes, I. M., Henriques-Silva, R., Penha, J., Zuanon, J., & Peres-Neto, P. R. 2014. Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities. *Ecography* 37: 464-475.
- France, R. L. 2012. Omnivory, vertical food-web structure and system productivity: Stable isotope analysis of freshwater planktonic food webs. *Freshwater Biology*, 57, 787–794.
- Fry, B. 2013. Alternative approaches for solving underdetermined isotope mixing problems. – *Mar. Ecol. Prog. Ser.* 472: 1–13.
- Gallardo, B., Garcia, M., Cabezas, A., Gonzalez, E., Gonzalez, M., Ciancarelli, C., and Comin, F. A. 2008. Macroinvertebrate patterns along environmental gradients and hydrological connectivity within a regulated river-floodplain. *Aquatic Sciences* 70: 248-258

- Gellner, G., & McCann, K. 2012. Reconciling the omnivory-stability debate. *The American Naturalist*, 179, 22–37.
- Holt, R. D. and Polis, G. A. 1997. A theoretical framework for intraguild predation. *Am. Nat.* 149, 745–764.
- Jardine, T. D., Hadwen, W. L., Hamilton, S. K., Hladyz, S., Mitrovic, S. M., Kidd, K. A., Tsoi, W. Y., Spears, M., Westhorpe, D. P., Fry, V. M., Sheldon, F. and Bunn, S. E. 2014. Understanding and overcoming baseline isotopic variability in running waters. *River Res. Applic.*, 30: 155-165. doi:10.1002/rra.2630
- Jackson, A. L. et al. 2011. Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. – *J. Animal Ecol.* 80: 595-602.
- Karaus, U., Alder, L., and Tockner, K. 2005. “Concave islands”: habitat heterogeneity of parafluvial ponds in a gravel-bed river. *Wetlands*. 25: 26-37
- Kidd, K.A. Schindler, D. W., Hesslein, R. H., and Muir, D. C. G. 1998. Effects of trophic position and lipid on organochlorine concentrations in fishes from subarctic lakes in Yukon Territory. *Can. J. Fish. Aquat. Sci.* 55, 869–881
- Kratina, P., LeCraw, R. M., Ingram, T., & Anholt, B. R. 2012. Stability and persistence of food webs with omnivory: Is there a general pattern? *Ecosphere*, 3, 1–18.
- Kuhn, N., and R. Amiet. 1988. Bundesinventar der Auengebiete von Nationaler Bedeutung, Eidg. Dep. Inners, Bundesamt fuer For. und Landschaftschutz, Abt. Natur und Heimatschutz, Bern, Switzerland.
- Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *Am. Nat.* 147, 784–812
- Loreau, M., Mouquet, N., and Gonzalez, A. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. *PNAS* 100: 12765-12770.
- Lytle, D. A., and Poff, N. L. 2004. Adaptation to natural flow regimes. *Trends in Ecology and Evolution*. 19: 94-100. doi: 10.1016/j.tree.2003.10.002
- Marcarelli, A. M., Baxter, C. V., Mineau, M. M. and Hall, R. O. 2011. Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology*, 92: 1215-1225. doi:10.1890/10-2240.1
- May, R. M. 1973. *Stability and Complexity in Model Ecosystems*. (Princeton University Press).
- May, R. M. 2001. *Stability and complexity in model ecosystems*. New Jersey, U.S.A.: Princeton University Press.
- McCutchan, J. H., Lewis, W. M., Kendall, C., and Mcgrath, C. C. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102: 378-390.
- McHugh P.A., McIntosh A.R. & Jellyman P.G. 2010. Dual influences of ecosystem size and disturbance on food chain length in streams. *Ecology Letters*, 13, 881–890.
- McPeck, M. A. 1998. The consequences of changing the top predator in a food web: a comparative experimental. *Ecological Monographs*, 68: 1-23.
- Meyns, S., R. Illi, and B. Ribl. 1994. Comparison of chlorophyll-a analysis by HPLC and spectrophotometry: Where do the differences come from? *Archiv für Hydrobiologie*, 132: 129–139
- Molnar, P.; Favre, Natalie; Perona, Paolo; Burlando, Paolo; Ruf, Wolfgang. 2008. Floodplain forest dynamics in a hydrologically altered mountain river. *Peckiana - Staatliche Museum für Naturkunde Goerlitz*, Vol. 5

- Moore, J. C., De Ruiter, P. C., and Hunt, H. W. 1993. Influence of Productivity on the Stability of Real and Model Ecosystems. *Science*: 906-908
- Mouquet, N., Munguia, P., Kneitel, J. M., and Miller, T. E. 2003. Community assembly time and the relationship between local and regional species richness. *Oikos* 103: 618-626.
- Opperman J. J., Luster, R., McKenney, B. A., Roberts, M., and Wrona Meadows, A. 2010. Ecologically functional floodplains: connectivity, flow regime and scale. *Journal of the American water resources association* 46: 211-226.
- Paillex, A., Castella, E., and Carron, G. 2007. Aquatic macroinvertebrate response along a gradient of lateral connectivity in river floodplain channels. *Journal North American Benthological Society* 26: 779-796.
- Perona, P., Camporeale, C., Perucca, E., Savina, M., Molnar, P., Burlando, P., and Ridolfi, L. 2009. Modelling river and riparian vegetation interactions and related importance for sustainable ecosystem management. *Aquat. Sci.* 71: 266 – 278
- Pfamatter, S. and P. Zanetta. 2003. Hydrogologie de la plaine alluviale du valmaggia entre bignasco et giugaglio (Tessin). Master's thesis, Universitt Lausanne.
- Philips, D. L., Inger, R., Bearhop, S., Jackson, A. L., Moore, J. W., Parnell, A. C., Semmens, B. X., and Ward, E. J. 2014. Best practices for use of stable isotope mixing models in food-web studies. – *Can. J. Zool.* 92: 823-835.
- Pimm S.L. 1982. *Food Webs*. Chapman and Hall, London.
- Pimm S. L., and Lawton, J. H. 1977. Number of trophic levels in ecological communities. *Nature* 268: 329–331.
- Pimm S.L., and Kitching R. L. 1987. The determinants of food chain lengths. *Oikos* 50: 302–307.
- Post D. M., Pace M. L., Hairston Jnr N. G. 2000. Ecosystem size determines food- chain length in lakes. *Nature* 405: 1047–1049.
- Post, D. M. 2002. The long and short of food-chain length. *Trends Ecol. Evol.* 17, 269–277.
- Post, D. M., and Takimoto, G. 2007. Proximate structural mechanisms for variation in food-chain length. *Oikos* 116, 775–782.
- R Core Team (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>
- Ruhí, A., Muñoz, I. , Tornés, E. , Batalla, R. J., Vericat, D. , Ponsatí, L. , Acuña, V. , Schiller, D. , Marcé, R. , Bussi, G. , Francés, F. and Sabater, S. 2016. Flow regulation increases food-chain length through omnivory mechanisms in a Mediterranean river network. *Freshw Biol*, 61: 1536-1549. doi:10.1111/fwb.12794
- Sabo J.L., Finlay J.C., and Post D. M. 2009 Food chains in freshwaters. *The Year in Ecology and Conservation Biology, 2009: Ann NY Acad Sci* 1162: 187–220.
- Sabo J.L.L., Finlay J.C.C., Kennedy T. & Post D.M.M. 2010. The role of discharge variation in scaling of drainage area and food chain length in rivers. *Science*, 330, 965–967.
- Saigo, M., Zilli, F.L., Marchese, M.R., and Demonte, D. 2015. Trophic level, food chain length and omnivory in the Paraná River: a food web model approach in a floodplain river system. *Ecological Research*. 30: 843. <https://doi.org/10.1007/s11284-015-1283-1>
- Schoener T.W. 1989. Food webs from the small to the large: the Robert H. MacArthur award lecture. *Ecology*, 70, 1559–1589.



- Schmitz, O. J., Hawlena, D. and Trussell, G. C. 2010. Predator control of ecosystem nutrient dynamics. *Ecology Letters*, 13: 1199-1209. doi:10.1111/j.1461-0248.2010.01511.x
- Singer, M. S., and Bernays, E. A. 2003. Understanding omnivory needs a behavioral perspective. *Ecology*, 84, 2532–2537.
- Smith, J. A., Mazumder, D., Suthers, L M., and Taylor, M. D. 2013. To fit or not to fit: evaluating stable isotope mixing models using simulated mixing polygons. – *Methods Ecol. Evol.* 4: 612–618.
- Stanford J.A., Lorang M.S. & Hauer F.R. 2005. The shifting habitat mosaic of river ecosystems. *Verhandlungen des Internationalen Verein Limnologie*, 29, 123– 136
- Stark., J. D., Boothroyd, I K. G., Harding, J. S., Maxted, J. R., and Scarsbrook, M. M. 2002. Protocols for sampling macroinvertebrates in wadeable streams. New Zealand Macroinvertebrate Working Group, Report no. 1. Prepared for the Ministry of the Environment. Sustainable Management Fund project no. 5103, 57 p.
- Tachet H., Bournaud M., Richoux P., and Usseglio-Polatera P. 2010. Invertébrés d'eau douce - systématique, biologie, écologie. CNRS Editions, Paris. Accessed through [www.freshwaterecology.info](http://www.freshwaterecology.info) - the taxa and autecology database for freshwater organisms, version 7.0 accessed on 23.02.2018.
- Takimoto, G., and Post, D. M. 2013. Environmental determinants of food-chain length: a meta-analysis. *Ecol. Res.* 28, 675–681
- Thomaz, S. M., Bini, L. M., and Bozelli, R. L. 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia* 579: 1-13
- Thompson, R. M., Hemberg, M., Starzomski, B. M., & Shurin, J. B. 2007. Trophic levels and trophic tangles: The prevalence of omnivory in real food webs. *Ecology*, 88, 612–617.
- Thompson, R. M. et al. 2012. Food webs: reconciling the structure and function of biodiversity. – *Trends. Ecol. Evol.* 27: 689-697.
- Tockner, K., Malard, F., Burgherr, P., Robinson, C. T., Uehlinger, U., Zah, R., Ward, J. V. 1997. Physico-chemical characterization of channel types in a glacial floodplain ecosystem (Val Roseg, Switzerland). *Archiv für Hydrobiologie* 140: 433–463.
- Tockner, K. and Stanford, J. A. 2002. Riverine flood plains: present state and future trends. *Environmental Conservation* 29: 308–330.
- Tockne , K., Pusch, M., Borchardt, D., and Lorang, M. S. 2010. Multiple stressors in coupled river-floodplain ecosystems. *Freshwater Biology* 55:135-151
- Tockner, K., Malard, F. and Ward, J. V. 2000. An extension of the flood pulse concept. *Hydrol. Process.*, 14: 2861-2883.
- Tockner, K., Pennetzdorfer, D., Reiner, N. , Schiemer, F. and Ward, J. V. 1999. Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river–floodplain system (Danube, Austria). *Freshwater Biology*, 41: 521-535
- Townsend C. R., Scarsbrook M. R., Dolédec S. 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams, *Limnology and Oceanography*, 42: 938-949
- Townsend, C.R., Thompson, R.M., McIntosh, A.R., Kilroy, C., Edwards, E. & Scarsbrook, M.R. 1998. Disturbance, resource supply, and food-web architecture in streams. *Ecol. Lett.*, 1, 200–209.

- Tunney, T. D., McCann, K. S., Lester, N. P., and Shuter, B. J. 2012. Food web expansion and contraction in response to changing environmental conditions. *Nature Communications*. 3:1105. doi: 10.1038/ncomms2098
- Uehlinger, U. 1991. Spatial temporal variability of the periphyton biomass in a prealpine river (Necker, Switzerland). *Archiv für Hydrobiologie* 123: 219–237.
- Vander Zanden, M. J., Shuter, B. J., Lester, N., and Rasmussen, J. B. 1999. Patterns of food chain length in lakes: a stable isotope study. *Am. Nat.* 154, 406–416
- Ward, C. L., McCann, K. S., and Rooney, N. 2015. HSS revisited: multi-channel processes mediation trophic control across a productivity gradient. *Ecol. Lett.* 18, 1190–1197
- Ward, C. L., and McCann, K. S. 2017. A mechanistic theory for food chain length. *Nature Communications*. 8:2028. doi: 10.1038/s41467-017-02157-0
- Warfe DM, Jardine TD, Pettit NE, Hamilton SK, Pusey BJ, et al. 2013. Productivity, Disturbance and Ecosystem Size Have No Influence on Food Chain Length in Seasonally Connected Rivers. *PLOS ONE* 8(6): e66240.
- Wentworth, C., K. 1922. A scale grade and class terms for clastic sediments. *The Journal of Geology*, 30:377-392
- Whited, D. C., Lorang, M. S., Harner, M. J., Hauer, F. R., Kimball, J. S. and Stanford, J. A. 2007. Climate, hydrologic disturbance, and succession: drivers of floodplain pattern. *Ecology*, 88: 940-953.
- Winemiller, K. O. 2005. Floodplain river food webs: generalizations and implications for fisheries management. *Proceedings of the second international symposium on the management of large rivers for fisheries*. Volume 2. Mekong river Commission, Phnom Penh, Cambodia: 285-312
- Wootton, K. L. 2017. Omnivory and stability in freshwater habitats: does theory match reality? *Freshwater Biology*. 62:821–832. DOI: 10.1111/fwb.12908

## Supporting Information

**Table S1.** Spearman rank correlations between potential drivers of food chain length (FCL).

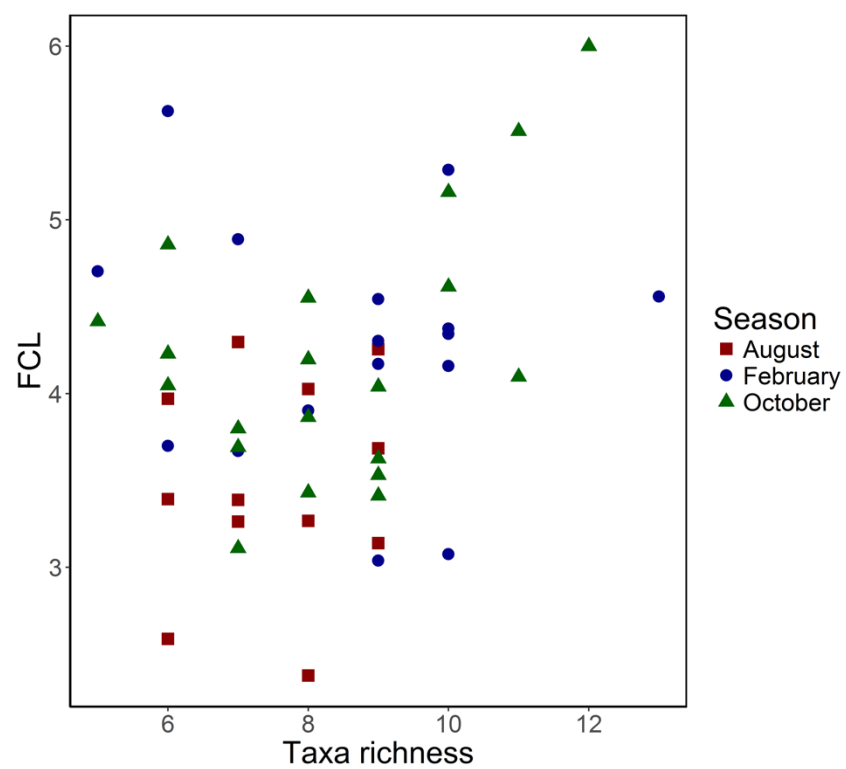
	<b>POM</b>	<b>Biofilm</b>	<b>Flood frequency</b>	<b>Time since last flood</b>
<b>Biofilm</b>	0.40			
<b>Flood frequency</b>	-0.07	-0.40		
<b>Time since last flood</b>	-0.07	0.21	-0.27	
<b>Habitat size</b>	-0.35	-0.31	0.43	-0.05

**Table S2.** Taxa identified during our three sampling events and respective functional feeding group, derived from Tachet et al. (2010). c = primary consumers; p = predators.

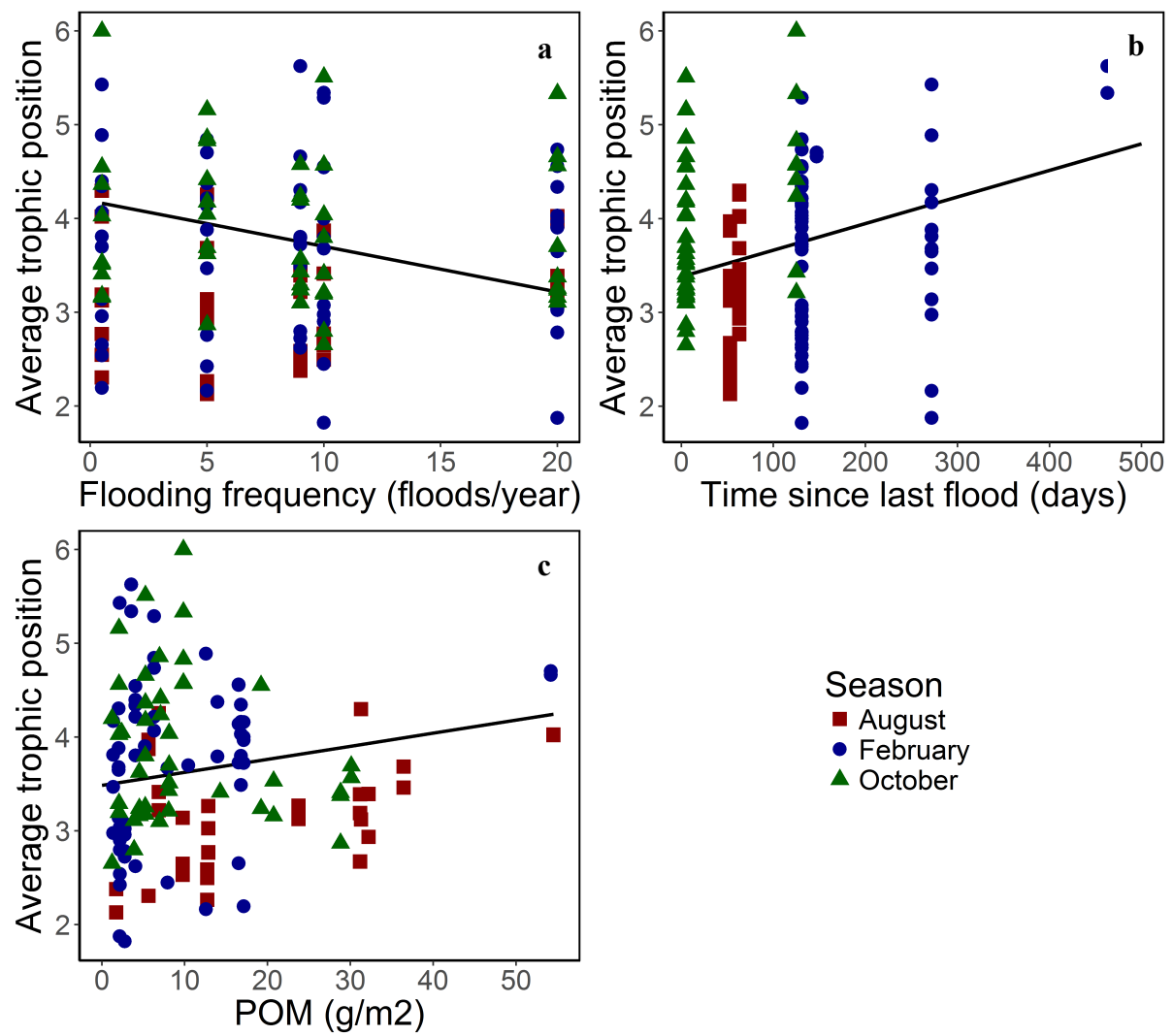
<b>Taxa</b>	<b>Feeding group</b>
Acarina	c
Atherix	p
Baetidae	c
<i>Capnia</i>	c
Chironomidae	c
Chloroperlidae	c
Corixidae	c
Dytiscidae	p
Elmidae	c
<i>Ephemerella</i>	c
Habroleptoides	c
Haliplidae	c
Heptagenidae	c
Hydracarina	c
<i>Hydropsyche</i>	c
Hydroptilidae	c
<i>Isoperla</i>	p
Leuctridae	c
Limnephilidae	c
Limoniidae	p
Megaloptera	c
Orthocladinae	c
<i>Perla</i>	p
Polycentropodidae	p
Rhyacophilidae	p
Tabanidae	c
Tanypodinae	p
Tipulidae	c

**Table S3.** Statistical summary of the modelled values for time since last flood and flooding frequency.

<b>Time since last flood</b>	<b>Min</b>	<b>Max</b>	<b>Median</b>	<b>SD</b>	<b>Mean</b>	<b>CV (%)</b>
February	131	463	131	86.6	187.9	46
August	53	653	63	123.9	85.2	145
October	5	715	5	147.8	54.6	271
<b>Flood frequency (per year)</b>	0.5	18.0	8.9	5.8	10.2	0.6



**Figure S1.** Plot showing the relationship between taxa richness on food chain length (FCL).



**Figure S2.** GLMM plots showing the effects of flooding frequency (a), time since last flood (b) and particulate organic matter (POM; c) on the average trophic position of predators.

# Synthesis

## **The effect of hydrology on spatial heterogeneity in habitat conditions**

There is a consensus among scientists and managers that restoring or preserving discharge variability is a central aspect in floodplain ecological conservation. This is because the spatial heterogeneity in flooding is what creates and maintains the habitat mosaic and the diversity of ecological niches at the floodplain scale (Stanford et al. 2005, Datry et al. 2014). The role of floods can be broken down into two main modes of action: the large floods drive the creation of habitat templates and geomorphological complexity, and the smaller floods maintain different physico-chemical environments within this template through differences in hydrological connectivity and disturbance regimes. Hydrological connectivity (HC), be it vertical through groundwater or lateral through surface water connection, results in similar physico-chemical gradients. With high-HC habitats typically richer in dissolved oxygen, nutrients and thermally more stable (Amoros and Bornette 2002, Paillex et al. 2009, Scott et al. 2011, Larned and Datry 2013). Nutrient concentrations in parafluvial habitats also tend to increase with connectivity to the main channel and with groundwater seepage, but are also affected by water retention time as well as biological processes (Amoros and Bornette 2002, Brunke et al. 2003, Larned and Datry 2013).). In alluvial floodplains, lateral connectivity is often pulsed and therefore can be overlapping with disturbance frequency where habitats flooded frequently are more similar to the main channel in their physical attributes, whereas habitats flooded less often exhibit more pond-like characteristics and in some cases signs of habitat terrestrialization (Ward and Tockner 2001).

A large part of this study aimed at understanding the linkages between hydrology and environmental conditions within habitat patches. The combination of a field experiment, where newly created habitats differed only in terms of vertical connectivity, and field-based investigation, where both vertical and lateral connectivity gradients overlapped, enabled us to partially separate the effects of lateral HC through regular flooding and vertical HC, on different habitat conditions. In the natural system, I characterized habitat conditions in 24 parafluvial habitats (PFH) at different times of the year and showed that they exhibited great spatial variability in their physico-chemical attributes. First, PFH varied widely in terms of structural diversity and substrate size distribution and this was strongly affected by flooding frequency: frequently flooded sites resembled more the main channel in these attributes, with relatively coarse and heterogeneous bottom substrate. This is presumably because greater flooding frequency also equates to smaller topographical barriers between the habitat and the main channel and thus greater flow velocities during floods. The bottom substrate is therefore likely to be coarser and more heterogeneous in these high-flow areas, because it is more likely to be reworked and eroded during floods, in contrast to slow-flow areas where finer sediment is deposited. This would be in line with conceptual models of floodplain functioning, stating that habitats may experience different flow velocities during floods depending on their position relative to the main channel and the local topography (Amoros and Bornette 2002). Second, PFH varied in terms of chemical signatures, reflecting differences in vertical HC and also in time since last flood. I showed that immediately after the flood, habitats exhibited the chemical signatures of high-HC sites (high dissolved oxygen levels, cool temperatures, low electrical conductivity). This highlights the effect of flooding on ecological successions, where



parafluvial habitats are set on a slow ecological succession tending towards terrestrialization, with intermediate stages of decreasing connectivity to the main channel (Ward and Tockner 2001). By flushing PFHs and reconnecting them to the main channel, floods set them back along that trajectory.

Whilst physical attributes such as sediment size distribution and diversity were mostly affected by floods, I showed in both the natural system and the experiment that chemical attributes were mostly affected by connectivity to hyporheic flow paths. This was especially obvious in the experimental system where artificial ponds differed only in their level of HC to hyporheic flow paths and yet exhibited great variation in chemical signatures and thermal regimes. This in itself highlights the importance of groundwater-surface water interactions in sustaining habitat diversity within the floodplain. Before constructing the experiment, we originally expected that experimental ponds located closer to the main channel would be more connected to the hyporheos, but surprisingly this was not the case. Instead, what we identified as paleochannels enabled more remote sites to receive “younger” hyporheic water compared to some ponds in the immediate vicinity of the main channel that are comparatively isolated hydrologically. In some cases, a head difference in excess of 1.5 m was measured between the main channel and ponds located only ~ 5 m away. This somewhat contrasts with the generally simplistic view of interactions between groundwater and surface water in floodplains, which often describes the alluvial aquifer as a sheet of water which interacts with the surface water only where topographical depressions intersect it. Whilst this simplification is necessary for the needs of hydrological / hydrodynamic modelling, I showed that paleochannels and preferential flow paths are more the rule than the exception in this alluvial floodplain. Practice should therefore move towards their inclusion in conceptual and physical models. Finally, I showed that algal productivity was affected by both the flooding and the level of vertical HC. Indeed, algal productivity was higher at low-HC sites in the experiment, probably reflecting their higher nutrient content and warmer temperatures. Whereas in the floodplain, algal productivity was primarily negatively affected by flooding frequency, independently of physico-chemical control.

Overall, our research shows that the spatial heterogeneity in chemical attributes is largely driven by differences in vertical HC and by the time elapsed since last flood. But the degree of vertical HC appears to be largely independent of the distance to the main channel, instead, preferential flow paths in former channels can enable remote habitats to be hydrologically well connected. In contrast, physical attributes are primarily affected by flooding. This strongly suggests that the spatial heterogeneity in flooding and the high spatial heterogeneity in hydraulic conductivity of the gravel matrix and resulting complexity in groundwater-surface water interactions, should both be taken into account to optimize environmental diversity within floodplains.

## **The effect of hydrology on spatial heterogeneity in macroinvertebrate communities**

The role of floods, and HC in general, on biota has been at the center of ecological research in floodplains (Boulton et al. 1992, Tockner et al. 1999, Sheldon et al. 2002, Arscott et al. 2003). Depending on the floodplain characteristics, environmental heterogeneity can result more from the variety of water sources feeding different habitats, or more from variability

in HC (Ward and Tockner 2001). But often HC affects local environment and communities (through dispersal) simultaneously, which results in complex relationships between these three elements (Legendre and Trousselier 1998, Gallardo et al. 2008). This research enabled us to partially separate the effects of flooding on biota, into its direct physical effects on the one hand and its indirect effects through habitat changes on the other. This study also showed that, independently of flooding, vertical connectivity through the hyporheos has important effects on macroinvertebrate communities.

In chapter 1, I showed that, independently of habitat conditions, flooding frequency directly affected community composition, with Coleoptera and Diptera favouring low-flooding frequencies and EPT taxa favouring high flooding frequencies. In line with other studies, taxa richness was generally positively affected by flooding frequency (Ward et al. 2002, Tockner et al. 1999, Amoros and Bornette 2002, Gallardo et al. 2008), but this effect was mediated by a higher substrate structural diversity in frequently flooded sites, probably due to the higher diversity of ecological niches. Community evenness was also higher in frequently flooded sites, because resource availability was lower. This contrasted with findings of other studies (Gallardo et al. 2008), and I attributed this to the increased competition in these isolated habitats (Ward and Tockner 2001). Finally, the results of chapter 3 show that taxa found in high-HC, frequently flooded sites were specialist species, adapted to life in running waters.

Chemical signatures also differed with vertical HC and the time since last flood, and these differences in turn affected communities. This was especially obvious in the experimental system, where communities were mostly organized along the gradient of HC and associated chemical attributes, with EPT taxa favouring the well-oxygenated, cool, high-HC sites. Overall, our research suggests that flooding affects invertebrate communities directly through mechanical disturbance but also indirectly through changes in local habitat conditions.

## **The effect of hydrology on food web attributes**

Food chain length (FCL: maximum trophic position among all members of a food web) is a key attribute of food webs and is known to influence species diversity, community structure and stability (reviewed in Sabo et al. 2009). Researchers have traditionally examined whether FCL was more affected by ecosystem size, productivity or level of disturbance. Later studies suggested that a combination of these factors might rather be at play. Because FCL is such a central aspect of food webs, I asked which environmental factors best explained its variation within the floodplain. Here, I calculated FCL as the maximum trophic position within the invertebrate communities, and found that FCL was shorter in frequently flooded habitats and immediately after floods. It appeared that these changes in FCL were driven by predators feeding at lower trophic levels in these habitats (trophic omnivory), rather than deletion of species within the food chain. These results have potentially important implications for species conservation in alluvial floodplains. First, they show that predators can be maintained in these highly dynamic systems by adapting their diet to prey availability. Second, they suggest that by reducing the strength of trophic interactions, trophic omnivory might increase food web stability within the floodplain (Bellmore et al. 2015). For instance, by shifting their diets, omnivorous predatory taxa may enable depleted consumer populations to better recover from environmental disturbance (Singer and Bernays 2003, Abrams and Fung 2010, Wootton et al. 2017).

## **Temporal changes in the habitat mosaic and diversity patterns**

The main conceptual understanding of flood effect on habitat and biotic diversity is that floods reset ecological succession of habitats, and therefore causes a homogenization of abiotic conditions within the floodplain, followed by divergence during low-flow periods (Amoros and Bornette 2002, Thomaz et al. 2007, Starr et al. 2014). It is the combination of this resetting effect and the spatial heterogeneity in disturbance that maintains the mosaic of habitats at different successional stages (Bravard et al. 1986, Salo et al. 1986, Mouw et al. 2013, Whited et al. 2007). And because biotic communities differ between successional stages, it also maintains biodiversity (Castella et al. 1984, Copp 1989, Ward and Tockner 2001). In chapter 3, I showed that conditions may only be homogenized within subsections of the floodplain, and that flooding instead appears to increase heterogeneity between habitats at the floodplain scale (Chaparro et al. 2018). This somewhat nuances the traditional view and suggests instead that flood effect on habitat diversity at the floodplain scale is dependent both on flood magnitude but also on the geomorphological complexity of the system and therefore on the spatial scale considered. Because inundation patterns are tightly linked to topography and geomorphology, this suggests that the relationships between flood discharge and habitat diversity may be specific to each floodplain (Ward and Tockner 2001)

Similarly, I showed that flooding increased beta diversity and disrupted species-environment relationships and trait filtering. This contradicts the findings from a previous study, which found that flooding homogenized invertebrate communities in a river floodplain (Starr et al. 2014). Our results potentially suggest that the increase in beta diversity was not due to environmental filtering along the post-flood environmental gradients but more probably to stochastic distribution of species after the flood (Myers et al. 2015). It is likely that the immediate effect of a flood on beta diversity depends on the magnitude of the flood, the geomorphological complexity of the floodplain and the ability of species to resist high flows.

## **Temporal changes in metacommunity organization**

Metacommunities and the relative importance of the different structuring processes have previously been examined in floodplains for fish (Fernandes et al. 2014), plankton (Chaparro et al. 2018) and invertebrates (Tonkin et al. 2016). Ecological research on temporal shifts in metacommunity organization is only at its beginning, and results suggest that these shifts are often linked to temporal variations in connectivity levels (Sarremejane et al. 2017). Importantly, our study showed that the main metacommunity structuring models alternated between Mass Effects (ME) and Species Sorting (SS), and that the dominance of either model was tightly dependent on dispersal mode, landscape connectivity, assembly stage and initial community composition. These insights were gained through the contrasting results between the experiment and the survey. In the experiment, I found that communities were immediately structured by a combination of SS and ME, and after 45 days ME was dominant in a subset of the sites located in the immediate vicinity of a natural floodplain habitat. I found quite a different pattern in the floodplain, with initially stochastic community compositions at Days 11 and 25 after the flood, and SS gaining importance over time. This did not apply to aerial dispersers however, which were initially structured by ME at sites with high landscape connectivity, until SS also became the main structuring model at Day 41. The fundamental differences between temporal

sequences in metacommunity structure between the two systems highlighted the importance of initial community structure and stochasticity on metacommunity assembly processes. Specifically, in the natural system, aquatic dispersers that were randomly distributed by the flood were able to survive in their new environments under initially low SS (low competition, less harsh conditions), but unable to disperse overland and track environmental variability. As populations grew and environmental conditions potentially harshened, species were gradually filtered out by SS (a combination of pure environmental filtering and competition, see Cadotte and Tucker 2017), according to their specific habitat affinities. This only affected aquatic dispersers, because aerial dispersers were able to massively disperse from neighbouring habitats initially, until SS gained importance, probably as a result of increasing competition. In contrast, because new habitats were artificially created in the experiment, initial community compositions were not stochastic like after the flood but null across all habitats. This initial absence of resident species and intermediate dispersal rates meant that species could directly colonize favourable habitats, and that harsh conditions in the least productive habitats may have acted as quite a strong environmental filter in comparison to post-flood conditions in floodplain habitats, driving high SS.

These results showed that flooding disrupted environment-biota relationships by redistributing individuals randomly. But more importantly, I showed that the mechanisms of metacommunity assembly varied in time, and that the temporal shifts in these mechanisms depended on the initial community composition, the degree of landscape connectivity with respect to the dispersal ability of species, and the local environmental conditions.

## Management implications and research outlook

### Management implications

My research has direct management implications for the conservation of floodplain ecosystems. First, it shows that spatial heterogeneity in flood disturbance is paramount to sustaining diversity at the floodplain scale. Additionally, in regulated systems, flood frequency should be optimized with respect to ecological trajectories within habitats, so that the mosaic of successional stages is maintained. My results imply that if flooding occurs too rarely, increased algal biomass and harshening environmental conditions will drive the most sensitive specialist species to extinction and reduce beta and gamma diversity. But if flooding occurs too frequently, strong dispersers and sensitive rheophilic species will dominate and the predominantly lentic taxa would also be extirpated. Second, I showed that vertical hydrological connectivity plays a central role in maintaining the mosaic of physico-chemical conditions and biotic communities. This shows that the spatial complexity of groundwater – surface water interactions should be considered when developing flow regulation strategies. Finally, I showed that dispersal among habitats can have a major impact on structural and functional aspects of local communities and also potentially lead to increased stability in the face of disturbance. Most hydro-ecological studies in floodplains highlight the central role of flow variability and hydrological connectivity in conservation, here I argue that managers should also optimize landscape connectivity within floodplains. Specifically, by working together with experts to identify habitats that are pivotal for post-flood recolonization or that contribute disproportionately biotic diversity.

## Scientific implications

### *Predictive models for floodplain biota*

Establishing flow release strategies in regulated systems often requires the comparison of different scenarios, especially when a balance has to be struck between energy production and ecological health. This means that decision makers increasingly rely on predictive tools linking management actions to ecological outcomes, in order to enable cost-benefit analyses of different management scenarios. For the assessment of flow regulation effects in river reaches, these are often achieved with eco-hydraulic models where discharge values are first translated into local hydraulics with hydrodynamic models and ecological outcomes measured as the surface areas of potential hydraulic habitat for given species or guilds. In these models, habitat affinity is most often described as distributions of affinity scores for different values of flow velocity and water depth. This classic approach is not adapted to modelling flow – biota relationships in alluvial floodplains like the Maggia, partly because:

- Parafluvial habitats contribute disproportionately to floodplain biodiversity and should therefore be included in the assessment, yet given their predominantly lentic nature, local hydraulics will not explain ecological attributes during disconnection phases.
- Instead, inundation regime and vertical hydrological connectivity are driving ecological attributes in these habitats, and these are not captured in eco-hydraulic models
- Given the dynamic nature of these systems, a steady-state, snapshot of available habitat area is unlikely to fully capture environment-biota linkages. Instead, temporal changes in the processes affecting communities should be considered, especially with respect to disturbance-recovery cycles.
- In order to capture the mechanisms that maintain biodiversity at the floodplain scale, the connectivity among communities should be included, in order to fully understand how local communities are assembled.

Because ecological processes unlikely to be fully captured in a habitat affinity score (such as dispersal or biotic interactions) play such an important role in structuring floodplain communities, I argue that alluvial floodplains would be great laboratories to develop more ecologically-sound predictive models that ecologists are calling for (see Anderson et al. 2006, Lancaster et al. 2010, Shenton et al. 2012).

### *Metacommunities in dynamic landscapes*

Finally, given the importance of landscape connectivity and dispersal, and the temporal variation in environmental conditions and hydrological connectivity, I suggest that future ecological research in alluvial floodplains should focus on investigating temporal changes in metacommunity organization. By first investigating the spatial and temporal scales at which regional processes take place and how these processes contribute to sustaining structural and functional diversity. Second, by identifying sites that contribute disproportionately to dispersal and the recolonization of other habitats and may therefore be of high conservation value. And third, by examining the specific influence of post-flood community composition on temporal

changes in metacommunity organization, which would effectively tie the changes in metacommunity assembly to flood magnitude.

## References

- Abrams, P. A., and Fung, S. R. 2010. The impact of adaptive defence on top-down and bottom-up effects in systems with intraguild predation. *Evolutionary Ecology Research*, 12, 307–325.
- Amoros, C., & Bornette, G. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology* 47: 761-776.
- Anderson, K. E., A. J. Paul, E. McCauley, L. J. Jackson, J. R. post and R. M. Nisbet. 2006. Instream flow needs in streams and rivers: the importance of understanding ecological dynamics. *Frontiers in Ecology and the Environment*. 4:309-318.
- Arscott, D. B., K. Tockner and J. V. Ward, 2003. Spatio-temporal patterns of benthic invertebrates along the continuum of a braided Alpine river. *Archiv für Hydrobiologie* 158: 431 – 460.
- Bellmore, J. R., Baxter, C. V. and Connolly, P. J. 2015. Spatial complexity reduces interaction strengths in the meta-food web of a river floodplain mosaic. *Ecology* 96: 274-283. doi:10.1890/14-0733.1.
- Boulton, A. J., C. G. Peterson, N. B. Grimm and S. G. Fisher, 1992. Stability of an aquatic macroinvertebrate community in a multiyear hydrologic disturbance regime. *Ecology* 73: 2192-2207.
- Cadotte, M. V. and Tucker, C. M. 2017. Should environmental filtering be abandoned? *Trends in Ecology and Evolution*, 32:429:437
- Castella E., Richardot-Coulet M., Roux C., Richoux P. 1984. Macroinvertebrates as 'describers' of morphological and hydrological types of aquatic ecosystems abandoned by the Rhône River. *Hydrobiologia*, 119: 219–225.
- Chaparro G, Horváth Z, O'Farrell I, Ptacnik R, Hein T. 2018. Plankton metacommunities in floodplain Islands under contrasting hydrological conditions. *Freshwater Biol.*63:380–391.
- Copp G.H. 1989. The habitat diversity and fish reproductive function of floodplain ecosystems. *Environmental Biology of Fishes* 26: 1-27.
- Datry, T., Corti, R., Belletti, B. and Piégay, H. 2014. Ground-dwelling arthropod communities across braided river landscape mosaics: a Mediterranean perspective. *Freshw Biol.* 59: 1308-1322.
- Fernandes, I. M., Henriques-Silva, R., Penha, J., Zuanon, J., and Peres-Neto, P. R. 2014. Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities. *Ecography* 37: 464-475.
- Gallardo, B., Garcia, M., Cabezas, A., Gonzalez, E., Gonzalez, M., Ciancarelli, C., and Comin, F. A. 2008. Macroinvertebrate patterns along environmental gradients and hydrological connectivity within a regulated river-floodplain. *Aquatic Sciences* 70: 248-258.
- Lancaster, J. and B. J. Downes. 2010. Linking the hydraulic world of individual organisms to ecological processes: putting ecology into ecohydraulics. *River Research and Applications* 26: 385-403.
- Larned, S. T., and Datry, T. 2013. Flow variability and longitudinal patterns in parafluvial water chemistry, aquatic invertebrates and microbial activity. *Freshwater Biology* 58: 2126-2143.

- Legendre, P. and M. Troussellier, 1988. Aquatic heterotrophic bacteria – modelling in the presence of spatial auto-Correlation. *Limnology and Oceanography* 33: 1055-1067.
- Mouw, J. E., Chaffin, J. L., Whited, D. C., Hauer, F. R., Matson, P. L., and Stanford, J. A. 2013. Recruitment and successional dynamics diversify the shifting habitat mosaic of an Alaskan floodplain. *River Research and Applications* 29: 671-685.
- Myers, J. A., Chase, J. M., Crandall, R. M. and Jiménez, I. 2015. Disturbance alters beta-diversity but not the relative importance of community assembly mechanisms. *J Ecol*, 103: 1291-1299.
- Paillex, A., Doledec, S., Castella, E., and Méricoux, S. 2009. Large river floodplain restoration: predicting species richness and trait responses to the restoration of hydrological connectivity. *Journal of Applied Ecology* 46: 250-258.
- Sabo J.L., Finlay J.C., and Post D. M. 2009 Food chains in freshwaters. *The Year in Ecology and Conservation Biology*, 2009: Ann NY Acad Sci 1162: 187–220.
- Salo, J., Kalliola, R., Haikkinen, I., Mäkinen, Y., Niemela, P., Puhakka, M., and Coley, P.D. 1986. 'River dynamics and the diversity of Amazon lowland forests', *Nature* 322: 254–258. Doi: 10.1038/322254a0
- Sarremejane R, Cañedo-Argüelles M, Prat N, Mykrä H, Muotka T, and Bonada N. 2017. Do metacommunities vary through time? Intermittent rivers as model systems. *Journal of Biogeography* 44: 2752-2763.
- Scott, D. T., R. F. Keim, B. L. Edwards, C. N. Jones, and D. E. Kroes 2014. Floodplain biogeochemical processing of floodwaters in the Atchafalaya River Basin during the Mississippi River flood of 2011, *J. Geophys. Res. Biogeosci.* 119, 537-546.
- Sheldon, F., A. J. Boulton and J. T. Puckridge, 2002. Conservation value of variable connectivity: aquatic invertebrate assemblages of channel and floodplain habitats of a central Australian arid-zone river, Cooper Creek. *Biological Conservation* 103: 13-31.
- Shenton, W., N. R. Bond, J. D. L. Yn and R. M. Nally. 2012. Putting the “Ecology” into environmental flowa: ecological dynamics and demographic modelling. *Environmental Management* 50:1-10.
- Singer, M. S., and Bernays, E. A. 2003. Understanding omnivory needs a behavioral perspective. *Ecology* 84: 2532-2537.
- Stanford, J. A., M. S. Lorang and F. R. Hauer. 2005. The shifting habitat mosaic of river ecosystems. *Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen*. 29:123-136.
- Starr, S. M., Benstead, J. P. and Sponseller, R. A. 2014. Spatial and temporal organization of macroinvertebrate assemblages in a lowland floodplain ecosystem. *Landscape Ecology* 29:1017-1031.
- Thomaz, S. M., Bini, L. M., and Bozelli, R. L. 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia* 579: 1-13.
- Tockner, K., Pennetzdorfer, D., Reiner, N., Schiemer, F. and Ward, J. V. 1999. Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river–floodplain system (Danube, Austria). *Freshwater Biology*, 41: 521-535.
- Tockner, K., F. Schiemer, C. Baumgartner, G. Kum, E. Iigand, I. Zlimuller and J. V. Ward, 1999. The Danube restoration project: Species diversity patterns across connectivity



- gradients in the floodplain system. *Regulated Rivers-Research and Management* 15: 245-258.
- Tonkin, J., Stoll, S., Jähnig, S., and Hase, P. 2016. Contrasting metacommunity structure and beta diversity in an aquatic-floodplain system. *Oikos* 125: 686-697.
- Ward, J. V., and Tockner, K. 2001. Biodiversity: towards a unifying theme for river ecology. *Freshwater Biology* 6:807-819.
- Ward, J.V., K. Tockner, D.B. Arscott and C. Claret, 2002. Riverine landscape diversity. *Freshwater Biology* 47:517-539.
- Whited, D. C., Lorang, M. S., Harner, M. J., Hauer, F. R., Kimball, J. S. and Stanford, J. A. 2007. Climate, hydrologic disturbance, and succession: drivers of floodplain pattern. *Ecology* 88: 940-953.
- Wootton, K. L. 2017. Omnivory and stability in freshwater habitats: does theory match reality? *Freshwater Biology*. 62:821-832.