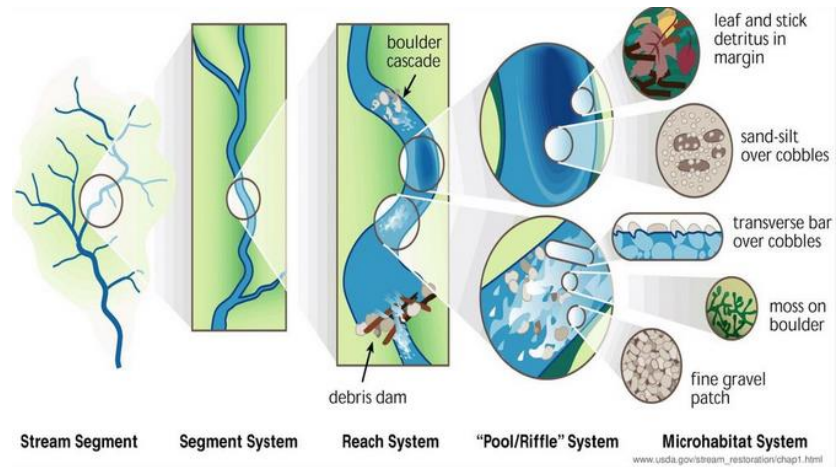


Ecology

Global Change Biology of Fluvial Ecosystems 2025

A role for hydraulic heterogeneity

Environmental heterogeneity across spatial scales



Stream and river beds are heterogeneous
Does heterogeneity (space and time) affect biodiversity and functions?

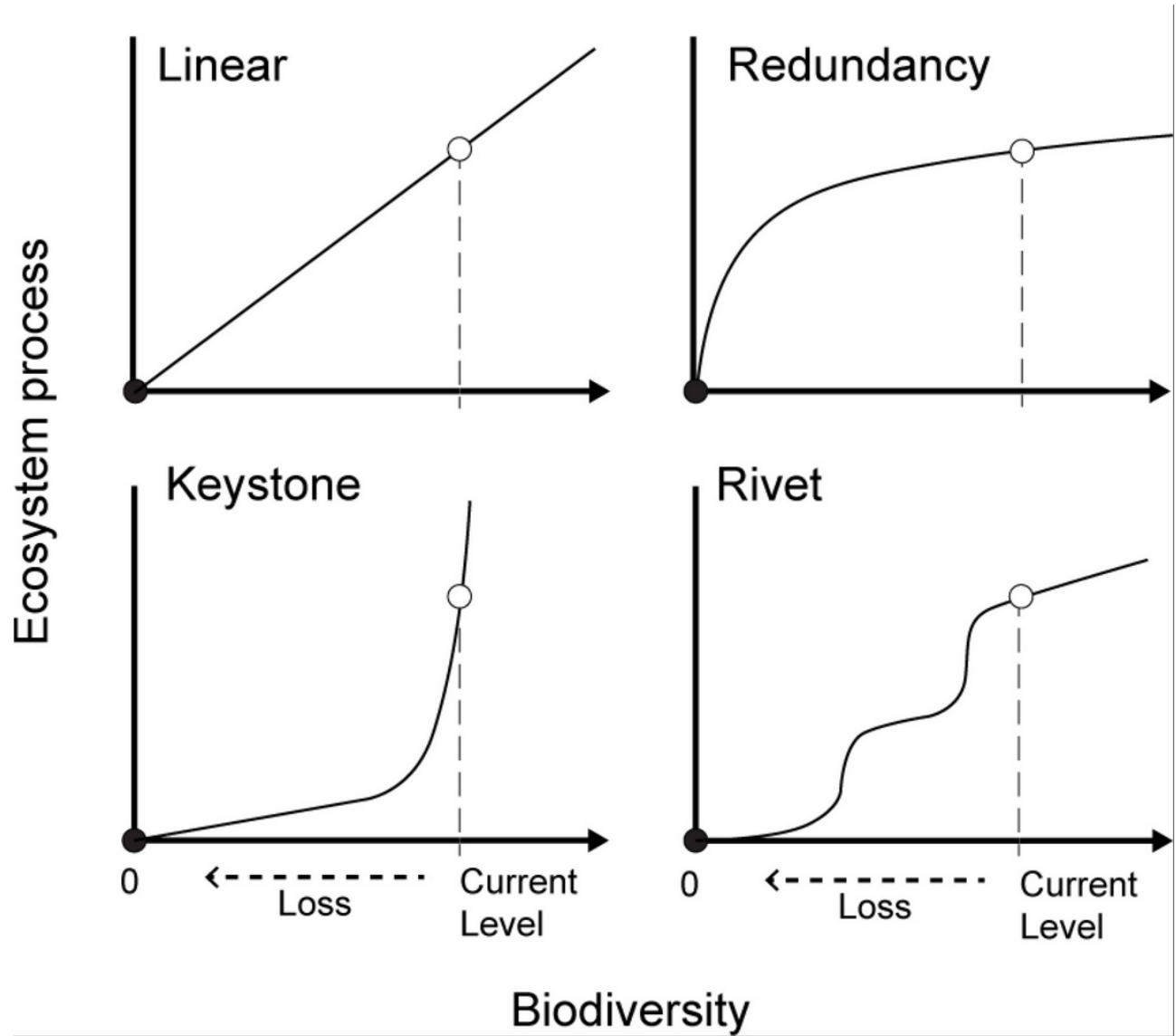


Relating biodiversity to ecosystem functioning
How do ecosystem functions/processes respond to biodiversity loss?

Conceptual models

Relating biodiversity to ecosystem functioning

How do ecosystem functions/processes respond to biodiversity loss?



Biodiversity effects in the wild are common and as strong as key drivers of productivity

J. Emmett Duffy¹, Casey M. Godwin² & Bradley J. Cardinale²

Evidence from experimental and observational studies that species richness increases biomass production across various systems.

How would this observation relate to monocultures?



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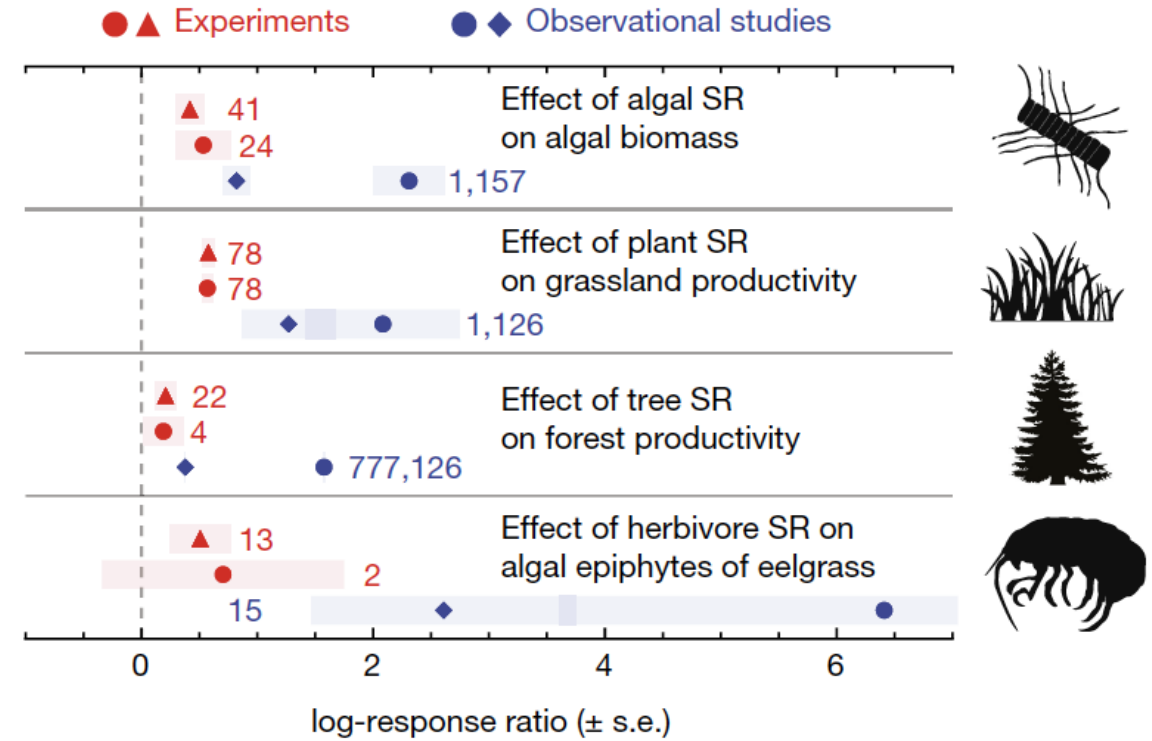


Figure 3 | Comparison of diversity effects on biomass production in observational versus experimental studies. Mean effect sizes are from experiments (red) and observational studies after accounting for covariates (blue). Observational estimates are calculated from the full dataset (circles) and over the narrower range of species richness (SR) used in experiments (diamonds). Triangles show log-response ratios calculated directly from experiments with ≥ 2 levels of species richness (without fitting a power function), whereas red circles show log response ratios calculated from the fitted power function. Numbers of experiments or sites included are shown. Horizontal bands denote standard errors. Extended Data Figs 1 and 2 show direct estimates of β and illustrate derivation of estimates, respectively.



Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges

M. Loreau,^{1*} S. Naeem,² P. Inchausti,¹ J. Bengtsson,³ J. P. Grime,⁴ A. Hector,⁵ D. U. Hooper,⁶ M. A. Huston,⁷ D. Raffaelli,⁸ B. Schmid,⁹ D. Tilman,¹⁰ D. A. Wardle⁴

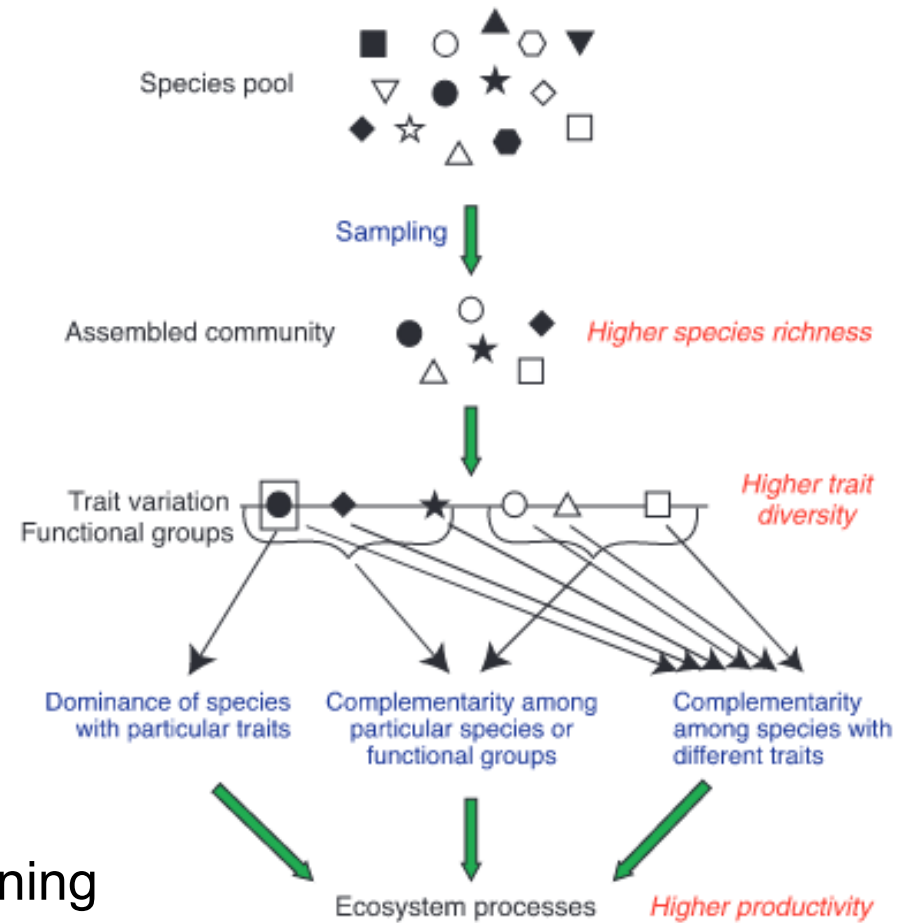


Fig. 2. Hypothesized mechanisms involved in biodiversity experiments using synthetic communities. Sampling effects are involved in community assembly, such that communities that have more species have a greater probability of containing a higher phenotypic trait diversity. Phenotypic diversity then maps onto ecosystem processes through two main mechanisms: dominance of species with particular traits, and complementarity among species with different traits. Intermediate scenarios involve complementarity among particular species or functional groups or, equivalently, dominance of particular subsets of complementary species.

Mechanisms underlying the relationship between biodiversity and ecosystem functioning

- Dominance or selection effect
- Complementarity

LETTER

doi:10.1038/nature09904

Biodiversity improves water quality through niche partitioning

Bradley J. Cardinale¹

Relating environmental heterogeneity to biodiversity and ecosystem functioning



Biodiversity improves water quality through niche partitioning

Bradley J. Cardinale¹

Disturbance/environmental heterogeneity

- Nitrate removal increases with species richness
- Algal biomass increases with richness
- Niche complementarity overwhelms; more diverse species drive nitrate removal

No disturbance/environmental 'homogeneity'

- Nitrate removal saturates with species richness
- Algal biomass saturates with richness
- Selection effects overwhelms; one dominant species drives nitrate removal

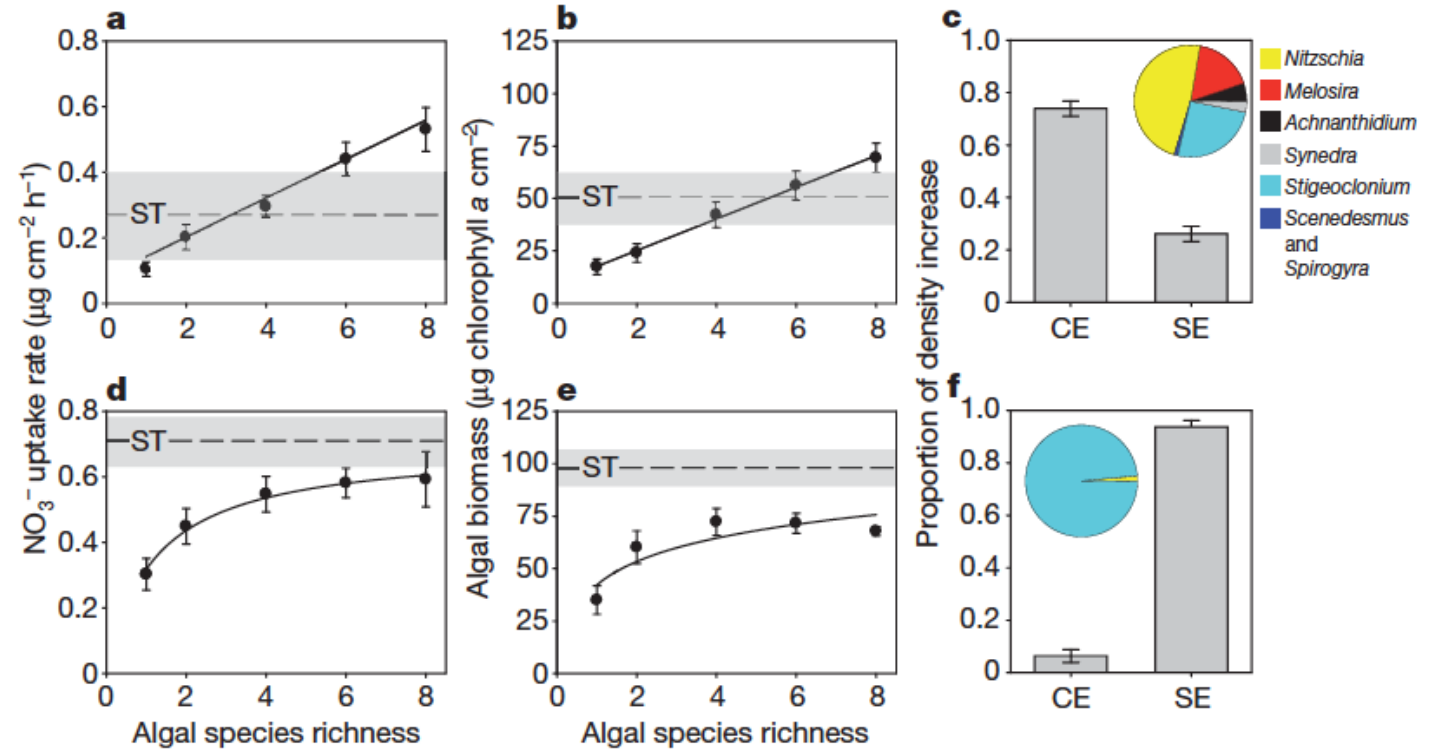


Figure 1 | Algal diversity effects on NO₃⁻, algal biomass and final population sizes. a–c, Heterogeneous streams, with flow varying spatially and habitats varying in successional age. d–f, Homogeneous streams, in which niche opportunities had been removed. Data are presented as mean ± s.e.m. of 24 replicates for monocultures, 15 replicates for 2–6 species polycultures and 6 replicates for 8-species polycultures. Best fitting functions (Table 1) are plotted

as solid lines. The horizontal line and the grey shaded area show mean ± s.e.m. for *Stigeoclonium*, which achieved the highest values of all of the monocultures. c, f, The proportion of increased polyculture cell densities driven by niche complementarity (CE) or selection effects (SE; that is, the influence of dominant species).

- Spatial and temporal heterogeneity
- Environmental and community turnover
- Intermediate disturbances across scales
- Niche diversification
- Avoidance of dominance
- Biodiversity and ecosystem functions



THE INFLUENCE OF SUBSTRATE HETEROGENEITY ON BIOFILM METABOLISM IN A STREAM ECOSYSTEM

BRADLEY J. CARDINALE,^{1,3} MARGARET A. PALMER,¹ CHRISTOPHER M. SWAN,¹ SHANE BROOKS,¹
AND N. LEROY POFF²

Homogenization of streambeds (environmental flows, regulation etc)

How would this affect community metabolism?

Experimental homogenization of the streambed (sediment distribution, associated hydraulics) at reach scale

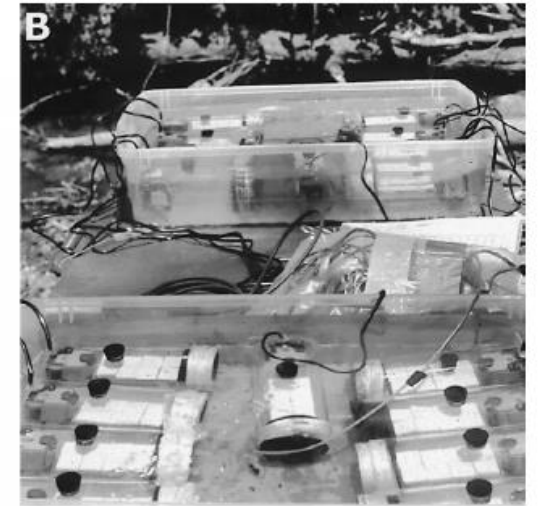
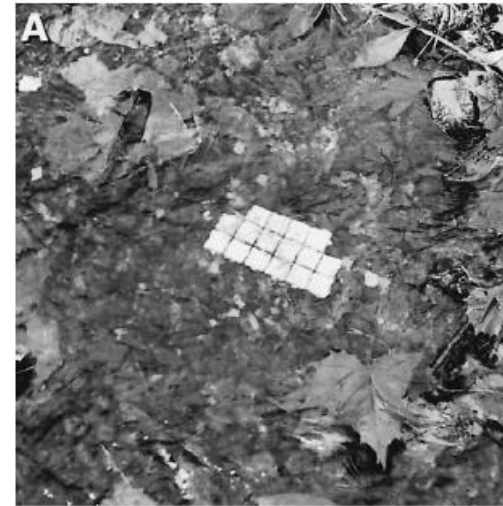


FIG. 1. (A) One of ten tile units that were placed on the benthic habitat of a low heterogeneity riffle. (B) The central incubation site showing tiles sealed inside 0.5-L metabolism chambers being held at a constant temperature in water baths. Also shown are examples of (C) low heterogeneity (LH) and (D) high heterogeneity (HH) riffles after manipulation of substrate variability.

THE INFLUENCE OF SUBSTRATE HETEROGENEITY ON BIOFILM METABOLISM IN A STREAM ECOSYSTEM

BRADLEY J. CARDINALE,^{1,3} MARGARET A. PALMER,¹ CHRISTOPHER M. SWAN,¹ SHANE BROOKS,¹
AND N. LEROY POFF²

LH: low heterogeneity reach
HH: High heterogeneity reach

- Median sediment size similar, spatial variance differs
- Elevated streambed roughness in HH reach

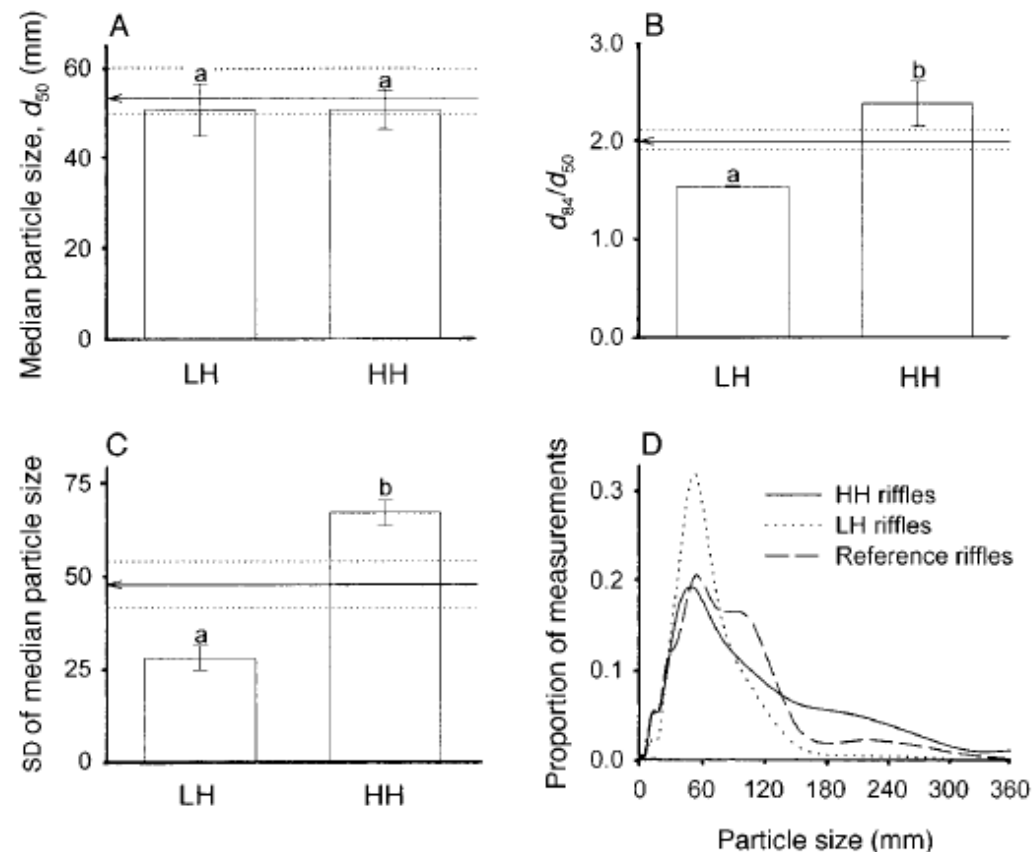
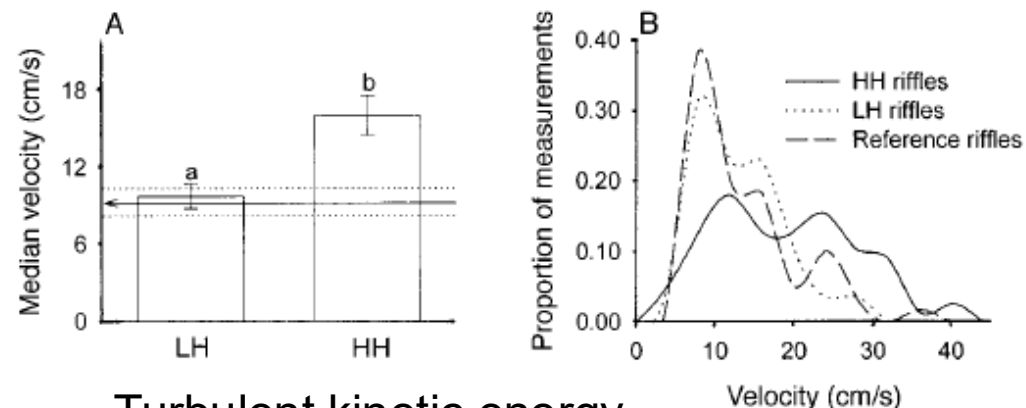


FIG. 2. (A) The median particle size in a riffle (d_{50}) and two measures of particle size heterogeneity: (B) the geomorphic ratio d_{84}/d_{50} , and (C) the standard deviation from the median particle size. Histograms show the means ± 1 SE for $N = 3$ low and $N = 4$ high heterogeneity riffles measured on day 20 of the experiment. Columns marked with different letters are significantly different from each other (t tests, $P < 0.05$). For comparison to natural characteristics of substrata in the stream, dotted lines show the maximum and minimum values, and the solid arrows show the mean value of $N = 3$ reference riffles that were not manipulated during the experiment. Also shown is (D) the frequency distribution of all particle measurements in the treatment and reference riffles. Smoothed trend lines are presented for clarity.

THE INFLUENCE OF SUBSTRATE HETEROGENEITY ON BIOFILM METABOLISM IN A STREAM ECOSYSTEM

BRADLEY J. CARDINALE,^{1,3} MARGARET A. PALMER,¹ CHRISTOPHER M. SWAN,¹ SHANE BROOKS,¹
AND N. LEROY POFF²

Flow velocity



Turbulent kinetic energy

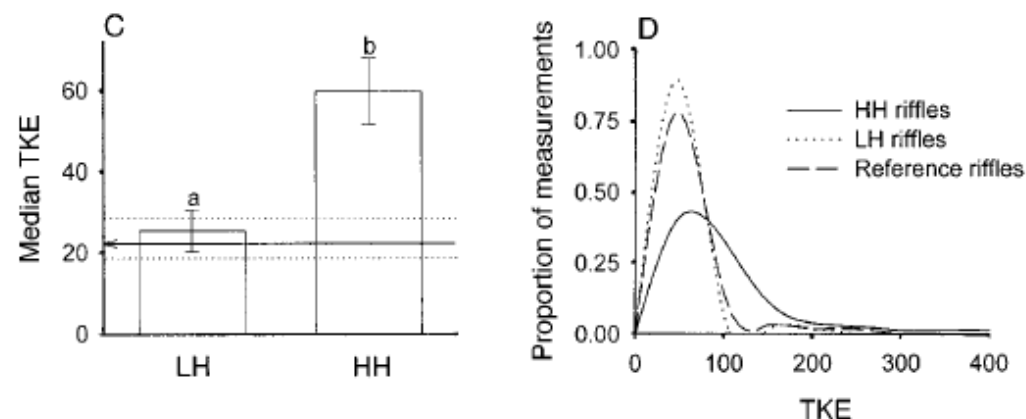


FIG. 3. (A) Median velocity, (B) the frequency distribution of velocity measurements, (C) median turbulent kinetic energy (TKE), and (D) the frequency distribution of TKE measurements in riffles on day 20 of the experiment. Data in plots (A) and (C) are mean values ± 1 SE of $N = 3$ low and $N = 4$ high heterogeneity riffles. Columns with different letters are significantly different from each other (t tests, $P < 0.05$). For comparison to natural characteristics of the stream, dotted lines show the maximum and minimum values, and the solid arrows show the mean value of $N = 3$ reference riffles that were not manipulated during the experiment. Data in plots (B) and (D) represent all measurements collected in the treatments and reference riffles with smoothed trend lines presented for clarity.

- Median flow velocity and turbulent kinetic energy (TKE) higher in HH reach
- TKE influences vertical mass transfer towards and through the laminar boundary layer
- Solute and gas replenishment for benthic biota

THE INFLUENCE OF SUBSTRATE HETEROGENEITY ON BIOFILM METABOLISM IN A STREAM ECOSYSTEM

BRADLEY J. CARDINALE,^{1,3} MARGARET A. PALMER,¹ CHRISTOPHER M. SWAN,¹ SHANE BROOKS,¹
AND N. LEROY POFF²

- Elevated respiration and gross primary production (GPP) in HH reach; same for biomass-specific GPP
- More hydraulic niches, elevated mass transfer
- Increased ecosystem processes

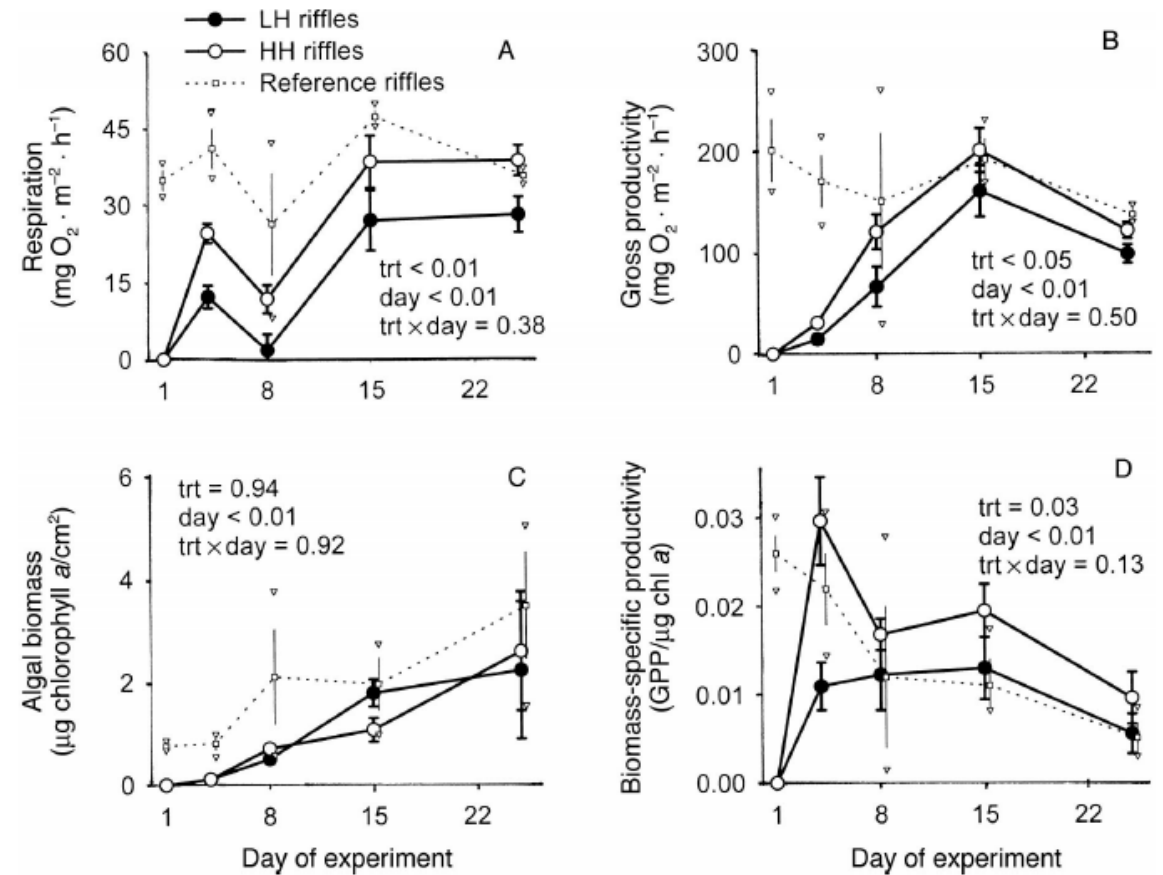


FIG. 4. (A) Respiration, (B) GPP, (C) algal biomass, and (D) biomass-specific productivity of the benthic biofilm on standardized ceramic tiles colonized in the riffle habitats. Data points are the mean \pm 1 SE of $N = 3$ low heterogeneity, $N = 4$ high heterogeneity, and $N = 3$ reference riffles. Open triangles show the maximum and minimum values for the reference riffles on each date. P values from repeated-measures ANOVAs comparing the LH and HH treatments are displayed for each variable. Mean temperatures during incubation of the tiles were held at ambient stream temperature (day 1 = 23.5°C, day 4 = 23.3°C, day 8 = 23.4°C, day 15 = 23.6°C, and day 25 = 24.7°C), and lighting conditions were identical for all tiles within a date (see *Methods*).

Environmental heterogeneity does matter for biodiversity and ecosystem processes and functioning

Human alterations reduce environmental heterogeneity, thereby reducing biodiversity and deteriorating ecosystem functioning



From the benthic to the hyporheic zone



Is the Hyporheic Zone Relevant beyond the Scientific Community?

Jörg Lewandowski ^{1,2,*}, Shai Arnon ³, Eddie Banks ⁴, Okke Batelaan ⁴, Andrea Betterle ^{5,6}, Tabea Broecker ⁷, Claudia Coll ⁸, Jennifer D. Drummond ⁹, Jaime Gaona Garcia ^{1,10,11}, Jason Galloway ^{1,2}, Jesus Gomez-Velez ¹², Robert C. Grabowski ¹³, Skuyler P. Herzog ¹⁴, Reinhard Hinkelmann ⁷, Anja Höhne ^{1,15}, Juliane Hollender ⁵, Marcus A. Horn ^{16,17}, Anna Jaeger ^{1,2}, Stefan Krause ⁹, Adrian Löchner Prats ¹⁸, Chiara Magliozzi ^{13,19}, Karin Meinikmann ^{1,20}, Brian Babak Mojarrad ²¹, Birgit Maria Mueller ^{1,22}, Ignacio Peralta-Maraver ²³, Andrea L. Popp ^{5,24}, Malte Posselt ⁸, Anke Putschew ²², Michael Radke ²⁵, Muhammad Raza ^{26,27}, Joakim Riml ²¹, Anne Robertson ²³, Cyrus Rutere ¹⁶, Jonas L. Schaper ^{1,22}, Mario Schirmer ⁵, Hanna Schulz ^{1,2}, Margaret Shanfield ⁴, Tanu Singh ⁹, Adam S. Ward ¹⁴, Philipp Wolke ^{1,28}, Anders Wörman ²¹ and Liwen Wu ^{1,2}

The hyporheic zone of streams and rivers

- Interface between surface and subsurface (groundwater) water
- Porous flow
- No light available
- Very large sedimentary surface area
- Biofilm growth
- Chemical gradients (redox)

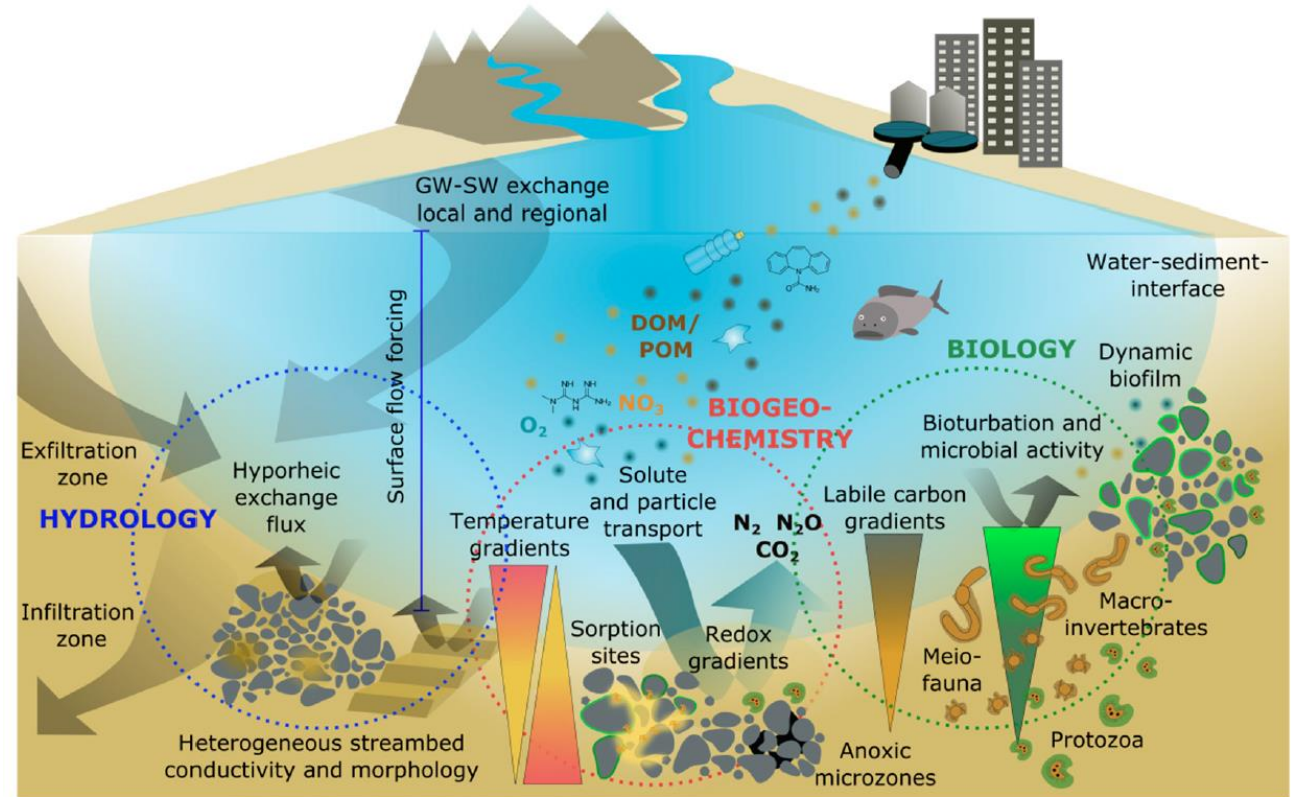


Figure 1. Conceptual model of the major hyporheic zone drivers and processes, as discussed in Section 2 of the present review. Dashed circles indicate the separation of disciplines in current hyporheic research, despite the high system complexity and manifold interconnections of hyporheic processes. GW-SW exchange is groundwater-surface water exchange; DOM and POM are dissolved or particulate organic matter, respectively.

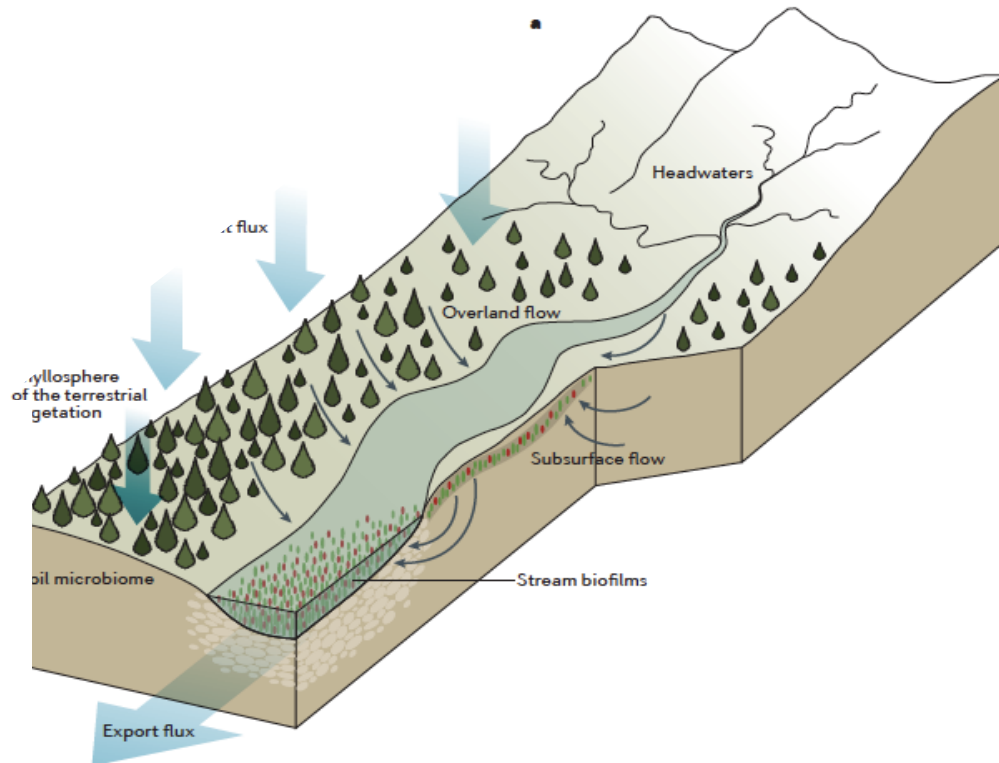
Streambed biofilms

The microbial skin of the catchment

MICROBIAL BIOFILMS

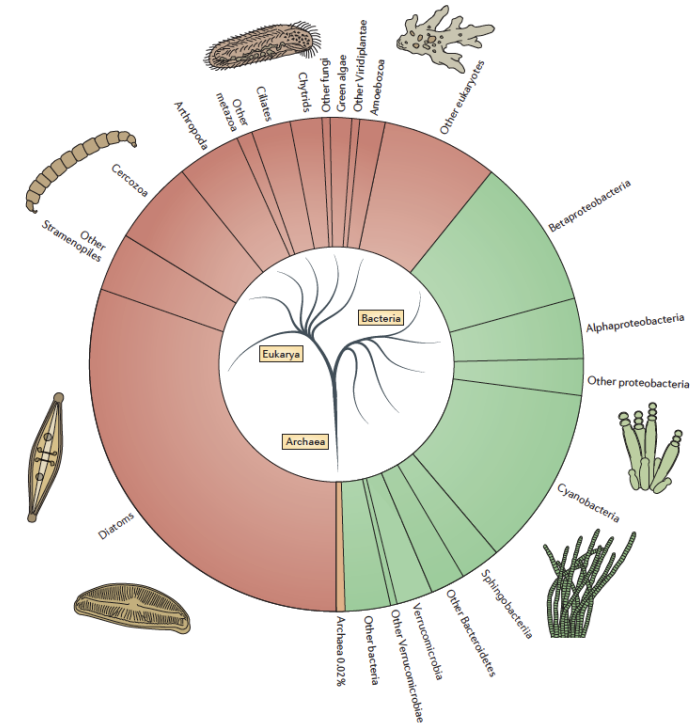
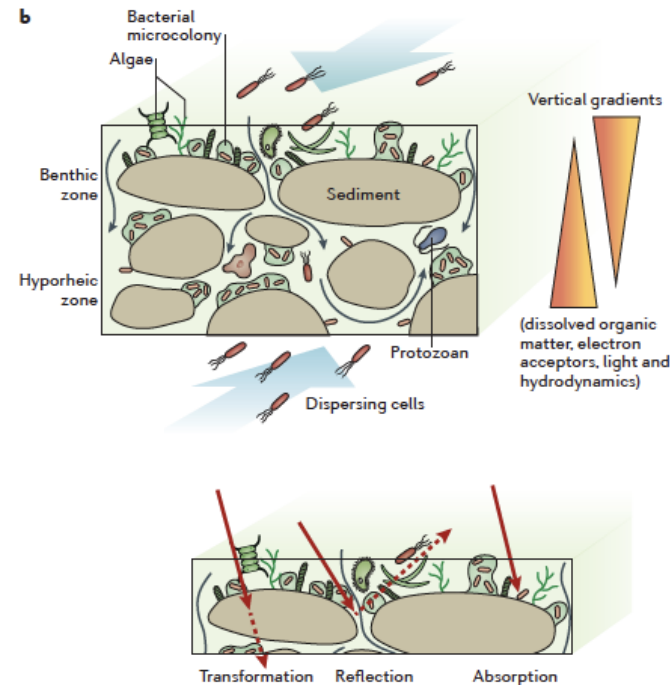
The ecology and biogeochemistry of stream biofilms

Tom J. Battin¹, Katharina Besemer², Mia M. Bengtsson³, Anna M. Romani⁴ and Aaron I. Packmann⁵



Stream biofilms

- Surface-attached microbial communities
- Encapsulated in a polymeric matrix
- Highly diverse — spanning all three domains of life, plus viruses
- Biofilm activity induces microscale chemical gradients within the streambed/hyporheic zone

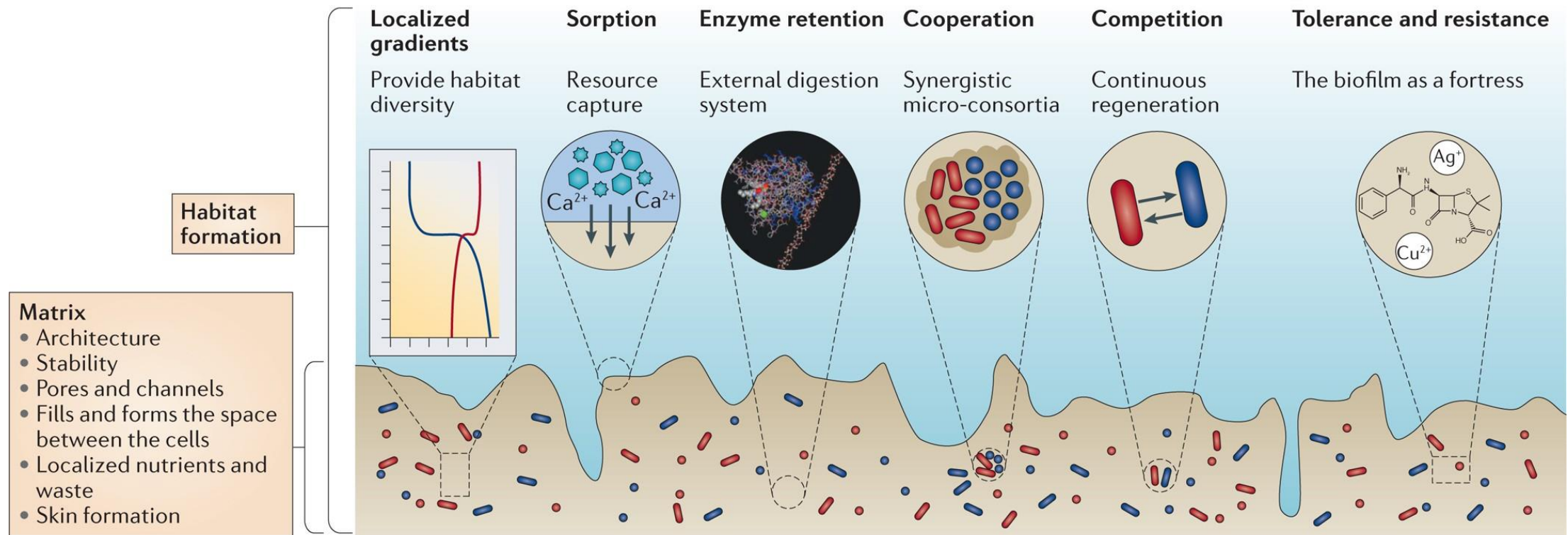


Biofilms: an emergent form of bacterial life

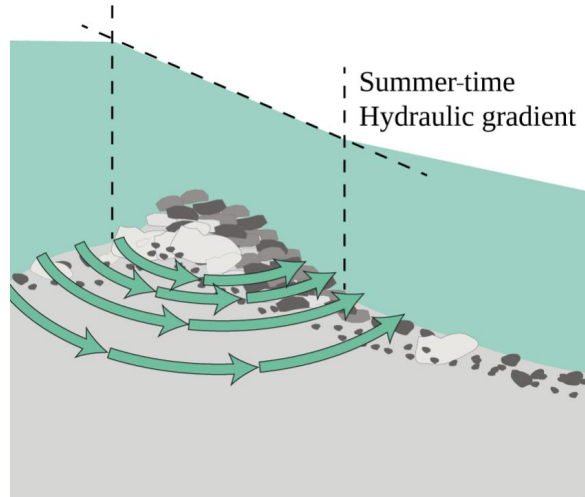
Hans-Curt Flemming¹, Jost Wingender¹, Ulrich Szewzyk², Peter Steinberg³, Scott A. Rice⁴ and Staffan Kjelleberg⁴

Advantages of the biofilm mode of life? (since 3.2 billion years)

- Largely mediated by the extracellular matrix (extracellular polymeric substances; EPS)
- Spatial proximity and biotic interactions
- Formation of micro-niches

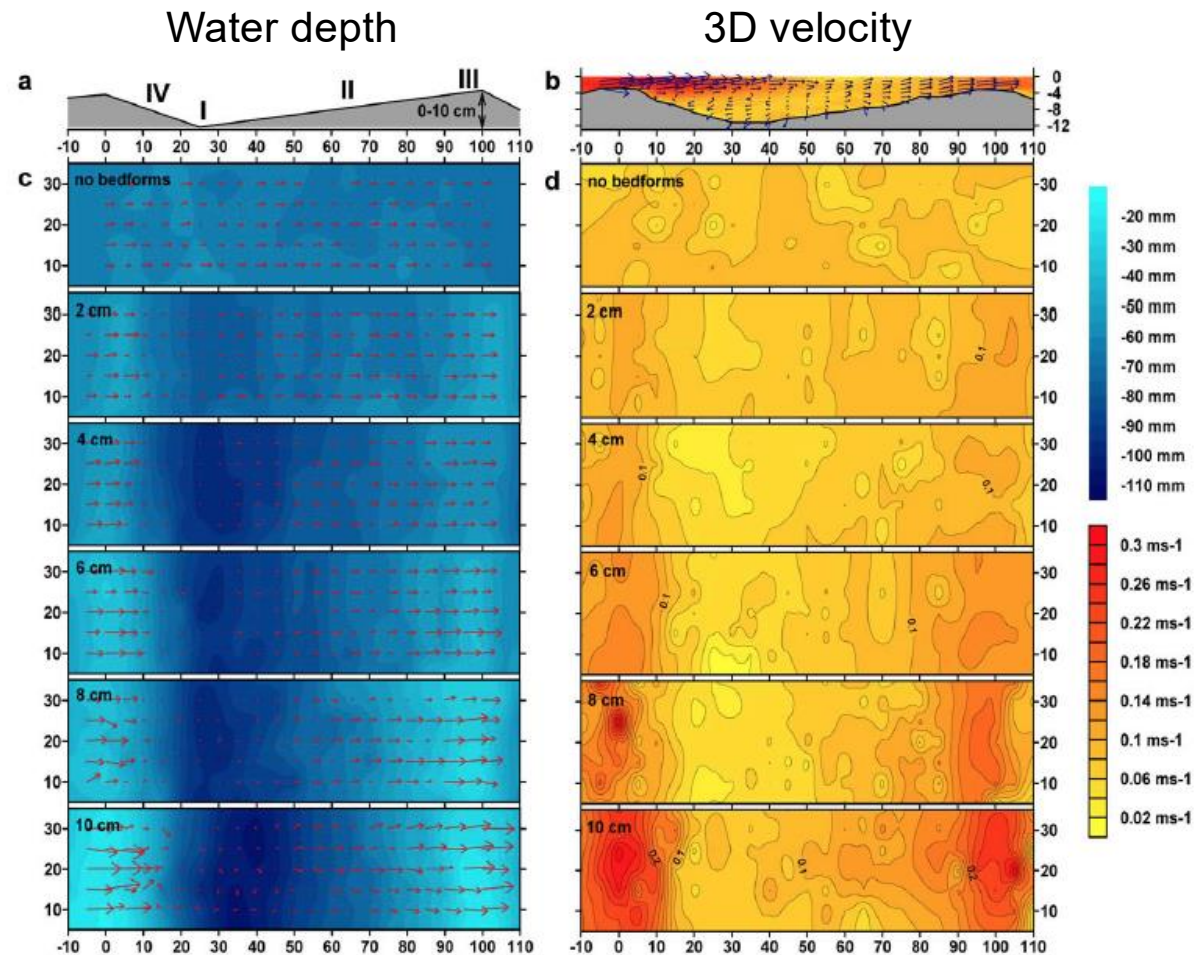


Bedforms impact near bottom hydraulics and biofilms



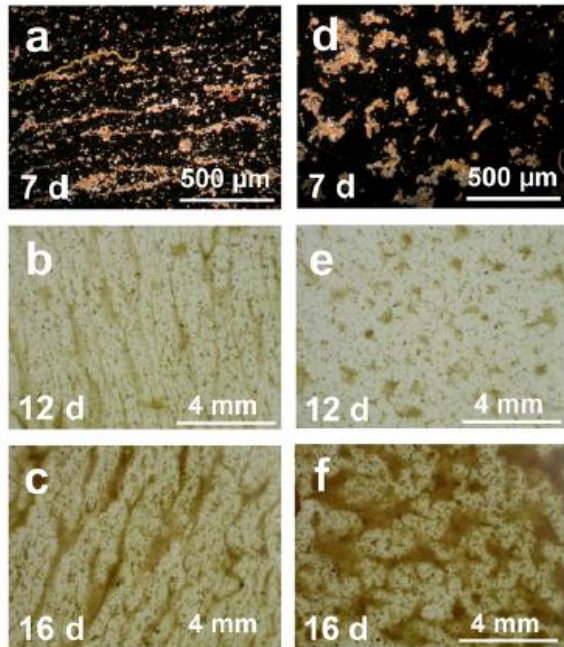
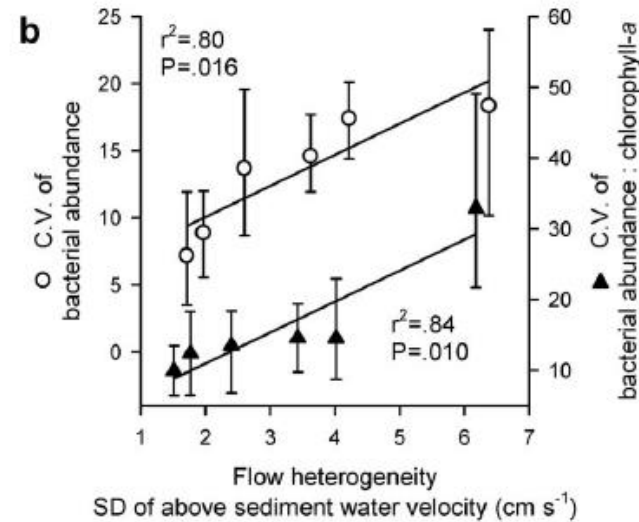
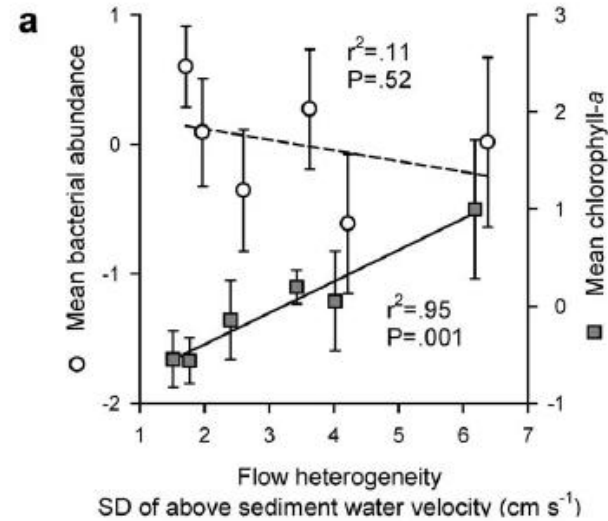
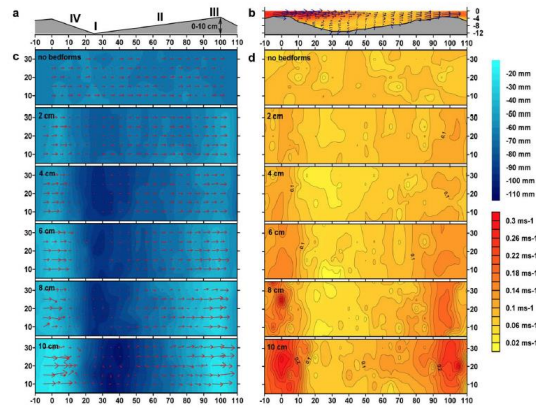
Physical Heterogeneity Increases Biofilm Resource Use and Its Molecular Diversity in Stream Mesocosms

Gabriel Singer^{1,2}, Katharina Besemer^{1,2}, Philippe Schmitt-Kopplin³, Iris Hödl^{1,2}, Tom J. Battin^{1,2*}



Physical Heterogeneity Increases Biofilm Resource Use and Its Molecular Diversity in Stream Mesocosms

Gabriel Singer^{1,2}, Katharina Besemer^{1,2}, Philippe Schmitt-Kopplin³, Iris Hödl^{1,2}, Tom J. Battin^{1,2*}

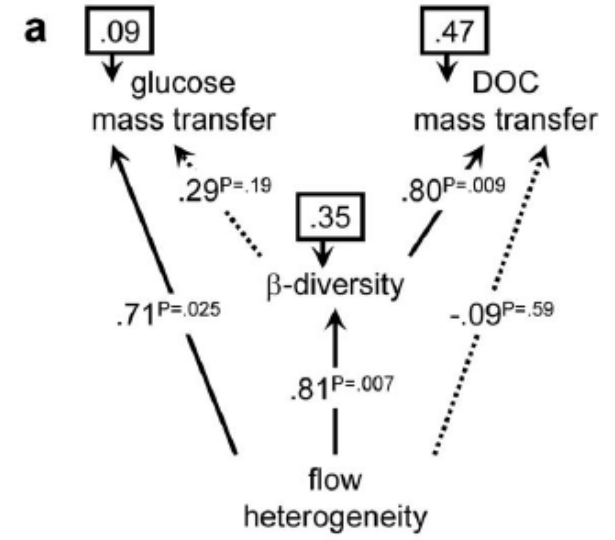
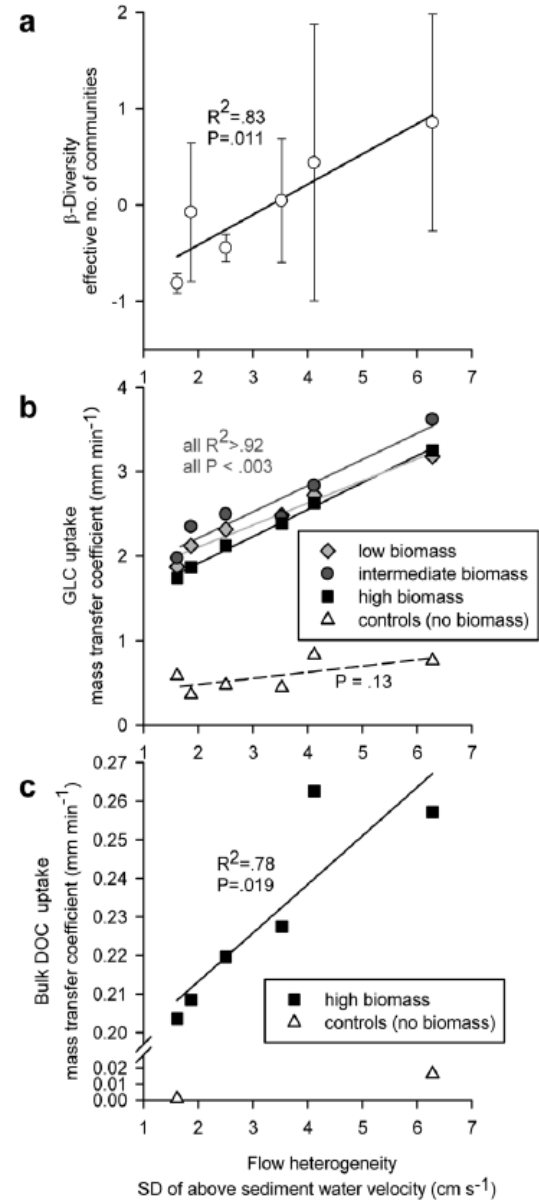
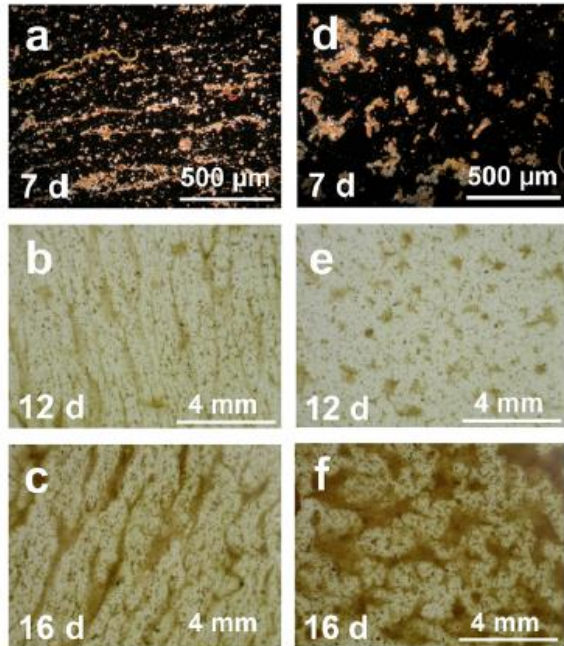
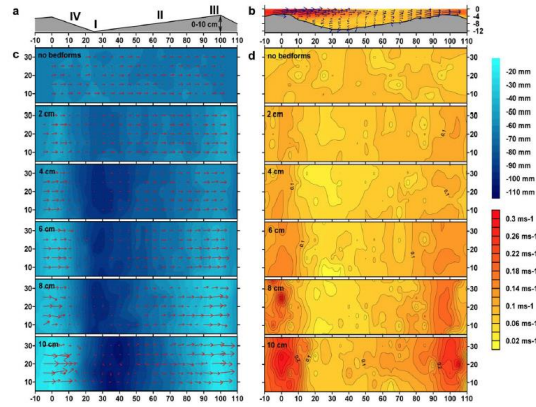


Flow heterogeneity promotes

- biofilm architectural heterogeneity (crest versus through)
- absolute algal biomass
- spatial variation of biomass (related to architecture)

Physical Heterogeneity Increases Biofilm Resource Use and Its Molecular Diversity in Stream Mesocosms

Gabriel Singer^{1,2}, Katharina Besemer^{1,2}, Philippe Schmitt-Kopplin³, Iris Hödl^{1,2}, Tom J. Battin^{1,2*}

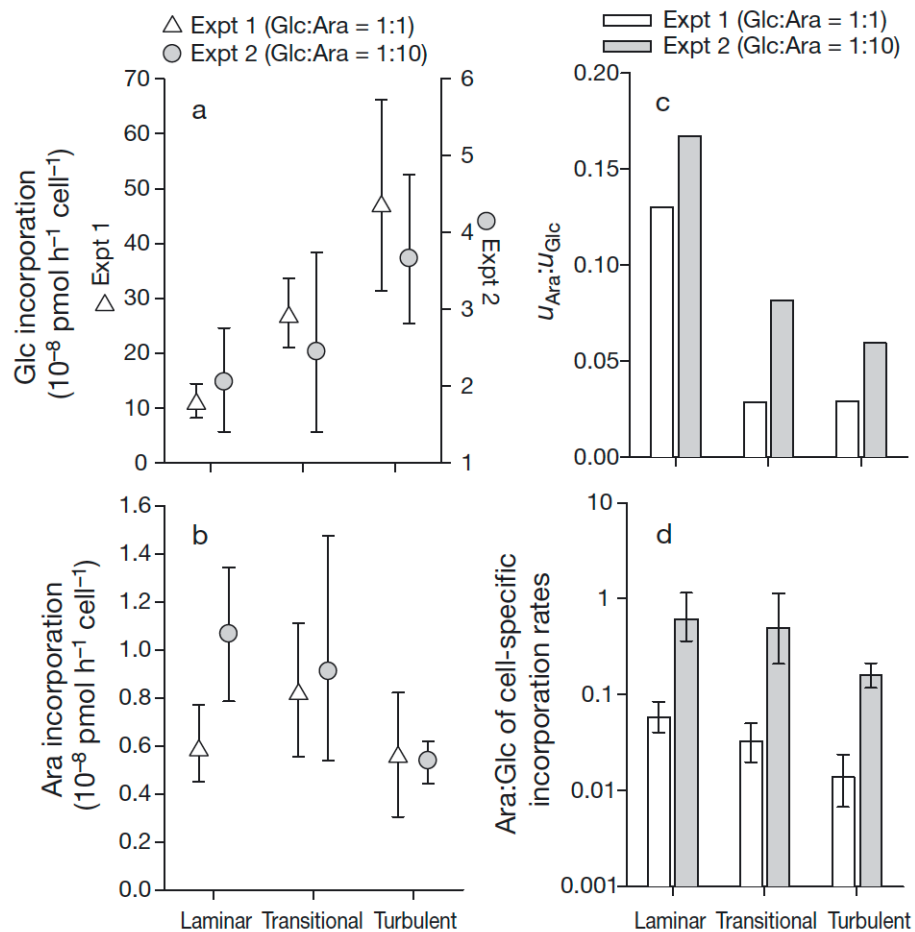


Flow heterogeneity promotes

- biofilm betadiversity
- uptake of glucose via mass transfer
- uptake of complex DOC via beta diversity
- more diverse DOC (not shown here)

Monomeric carbohydrate uptake and structure–function coupling in stream biofilms

Gabriel Singer^{1,2}, Katharina Besemer^{1,2}, Gerald Hochedlinger¹, Ann-Kathrin Chlup¹, Tom J. Battin^{1,2,*}

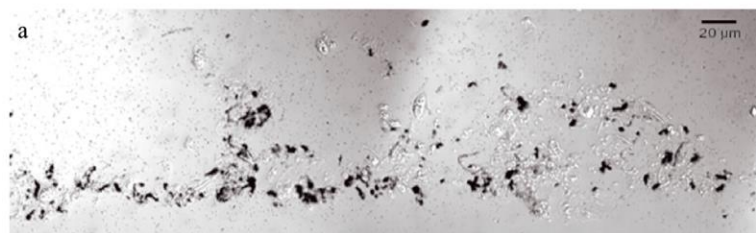


- Hydraulics affects sugar uptake rates
- Glucose: highly available to the microbial metabolism
- Arabinose: less available to the microbial metabolism
- Metabolic layering within biofilms (glucose versus arabinose)
- Hydraulic heterogeneity increases the width of DOC molecules removed from the water

A combination of physical and biological processes



Glucose:
upper layers of the biofilm

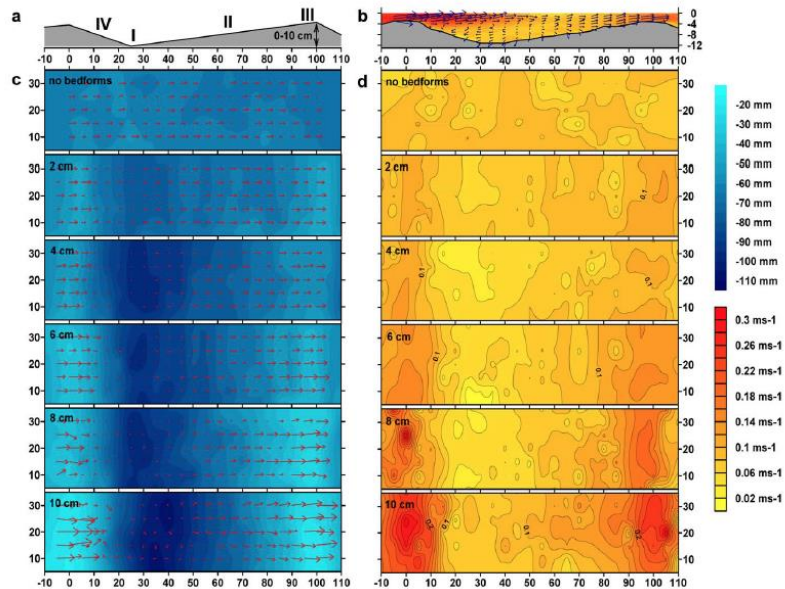


Arabinose:
throughout the entire biofilm



Mechanisms underpinning self-purification

- Spatial heterogeneity of streambed features and hydraulics
- Biofilm architecture (physical structure) and biomass
- Microbial diversity
- DOC uptake

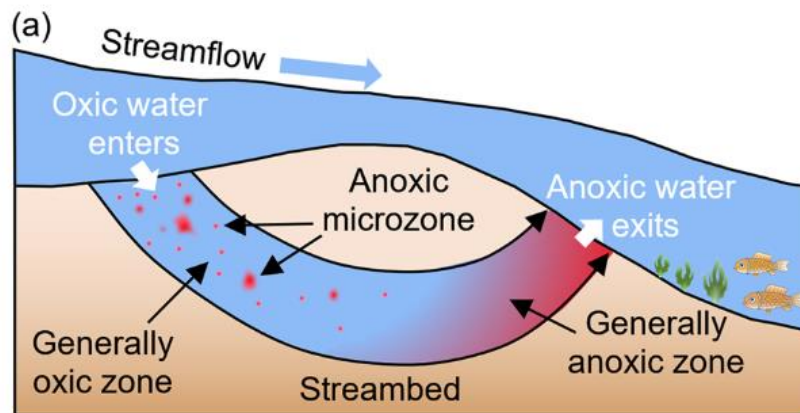
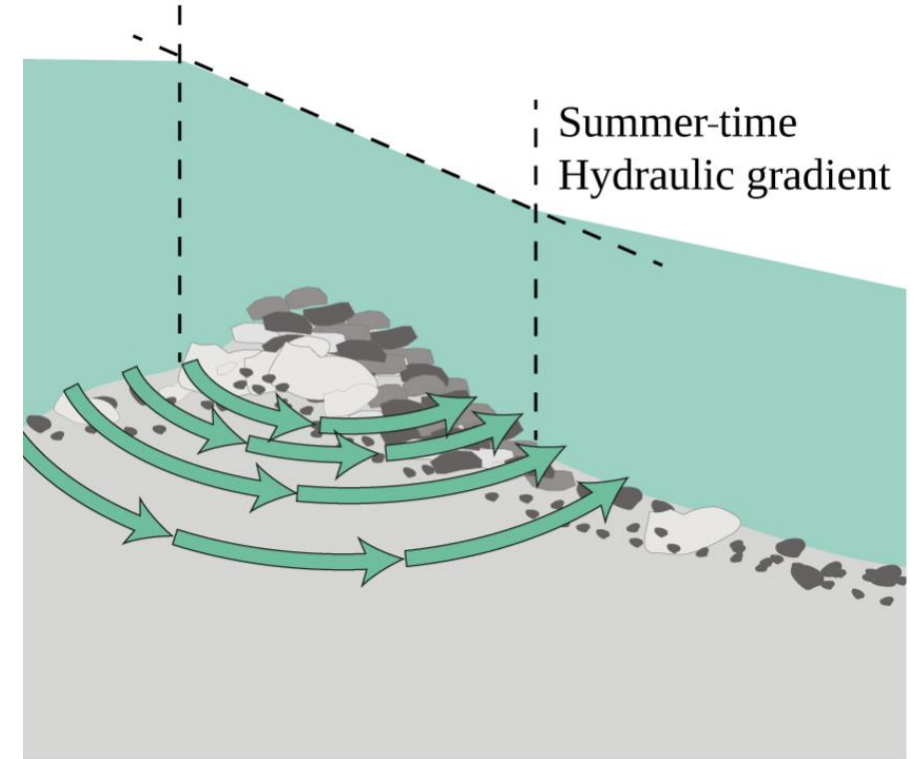


Bedform features and related hydraulic gradients promote hyporheic exchange

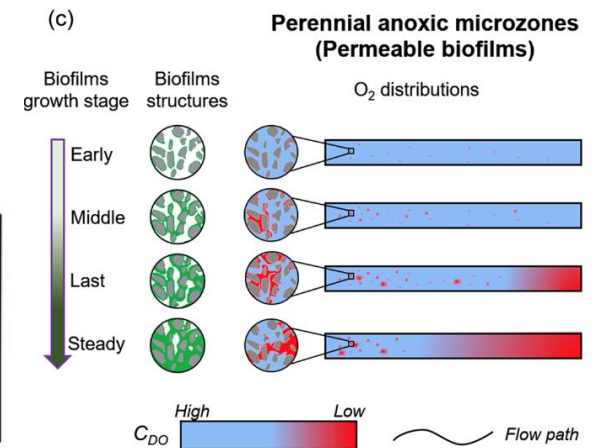
Advective transport of solutes and gases into the hyporheic zone — increased residence times (porous flow!) facilitate chemical reaction and microbial growth

Bedform features (i.e., roughness) also promote turbulence, hence gas (e.g., O₂) transfer through the water surface

Replenishing gas transport into the hyporheic zone — as a bioreactor



Geophysical Research Letters
 Research Letter | Free Access
 Permeable Biofilms Can Support Persistent Hyporheic Anoxic Microzones
 Yang Xian, Menggui Jin, Hongbin Zhan, Xing Liang



Key Points:

- The complexity of HZ rivers and controls exceeds the range of conditions considered in previous conceptualizations and model formulations
- Understanding organizational

Stefan Krause¹, Benjamin W. Abbott², Viktor Baranov³, Susana Bernal⁴, Phillip Blain¹, Thibault Datry⁵, Jennifer Drummond⁴, Jan H. Fleckenstein⁶, Jesus Gomez Velez⁷, David M. Hannah¹, Julia L. A. Knapp⁸, Marie Kurz⁹, Jörg Lewandowski¹⁰, Eugènia Martí⁴, Clara Mendoza-Lera¹¹, Alexander Milner¹, Aaron Packman¹², Gilles Pinay¹³, Adam S. Ward¹⁴, and Jay P. Zarnetzke¹⁵

The hyporheic zone as a bioreactor

- Increased residence times and inputs from various sources (e.g., surface water, groundwater)
- Transformation and greenhouse gas production
- Impacts for downstream biogeochemistry
- ‘Self-purification’ – removal of pollutants

Requires a holistic view across disciplines

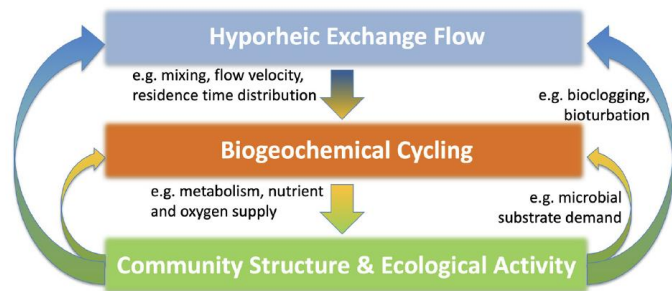
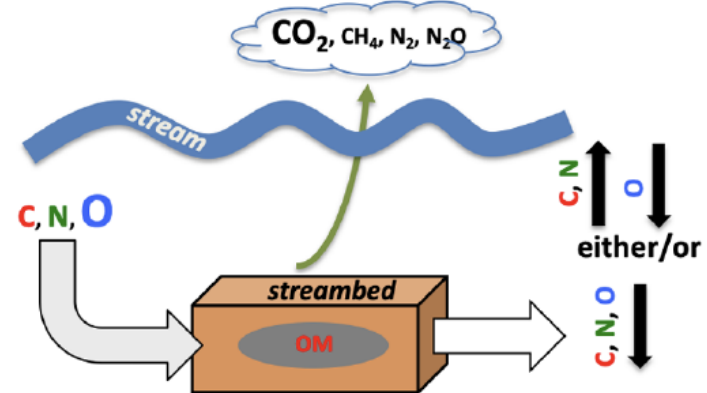
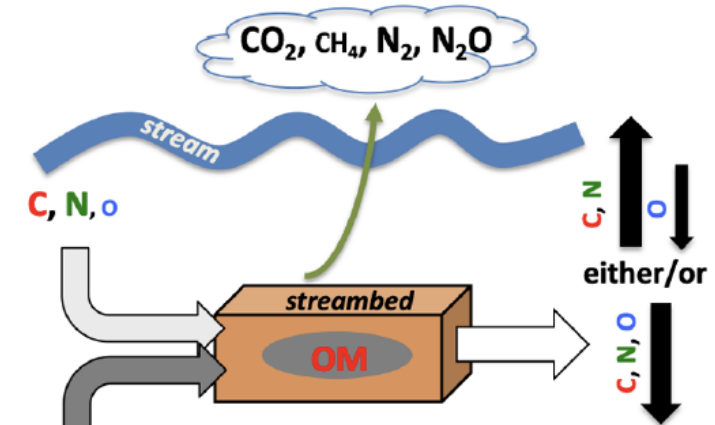


Figure 5. Multi-directional interactions between physical controls of hyporheic exchange flow, streambed biogeochemical cycling, and biological community structure and ecological (metabolic) functioning (red arrows), including ecological feedbacks on streambed biogeochemistry biogeochemistry [e.g., microbial demand for substrate shifting porewater from oxic to anoxic (aerobic to anaerobic metabolic pathways)] as well as hyporheic exchange (e.g., bioturbation, bioclogging, and ecosystem engineering).



(B)



(D) N

Restoring the bioreactor



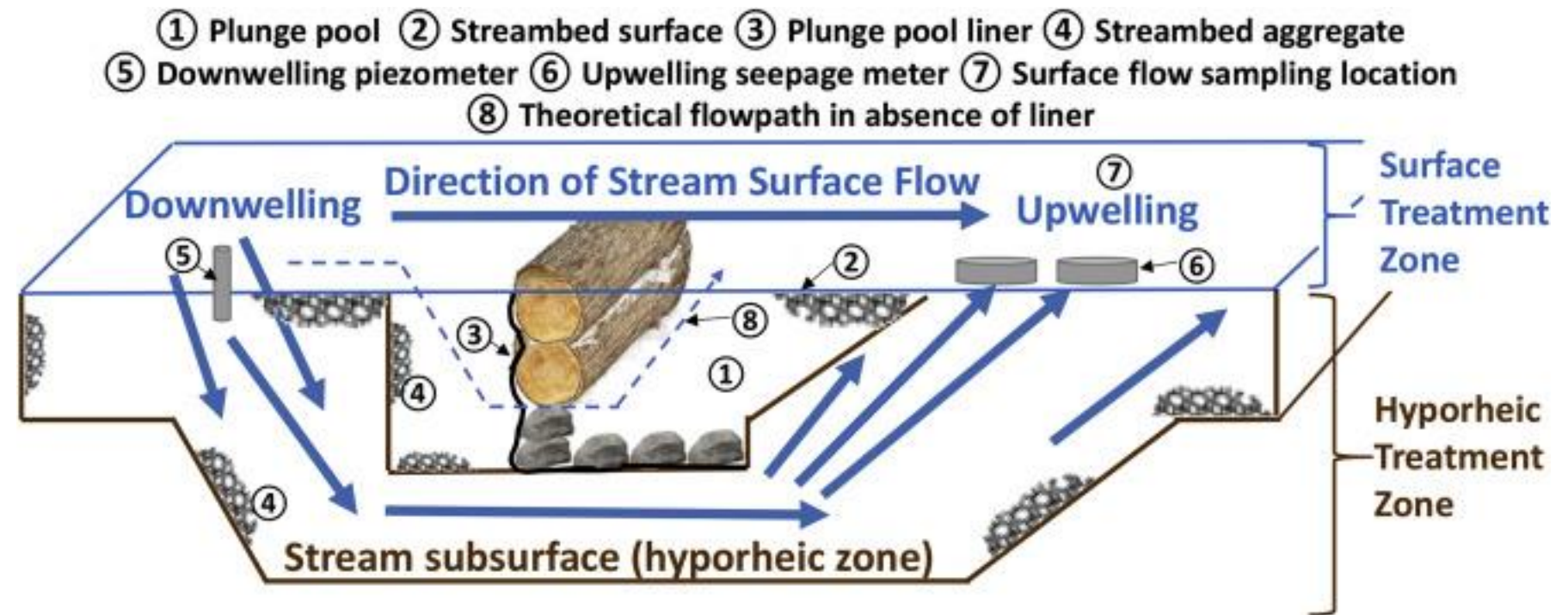
Water Research
Volume 150, 1 March 2019, Pages 140-152



Evaluating emerging organic contaminant removal in an engineered hyporheic zone using high resolution mass spectrometry

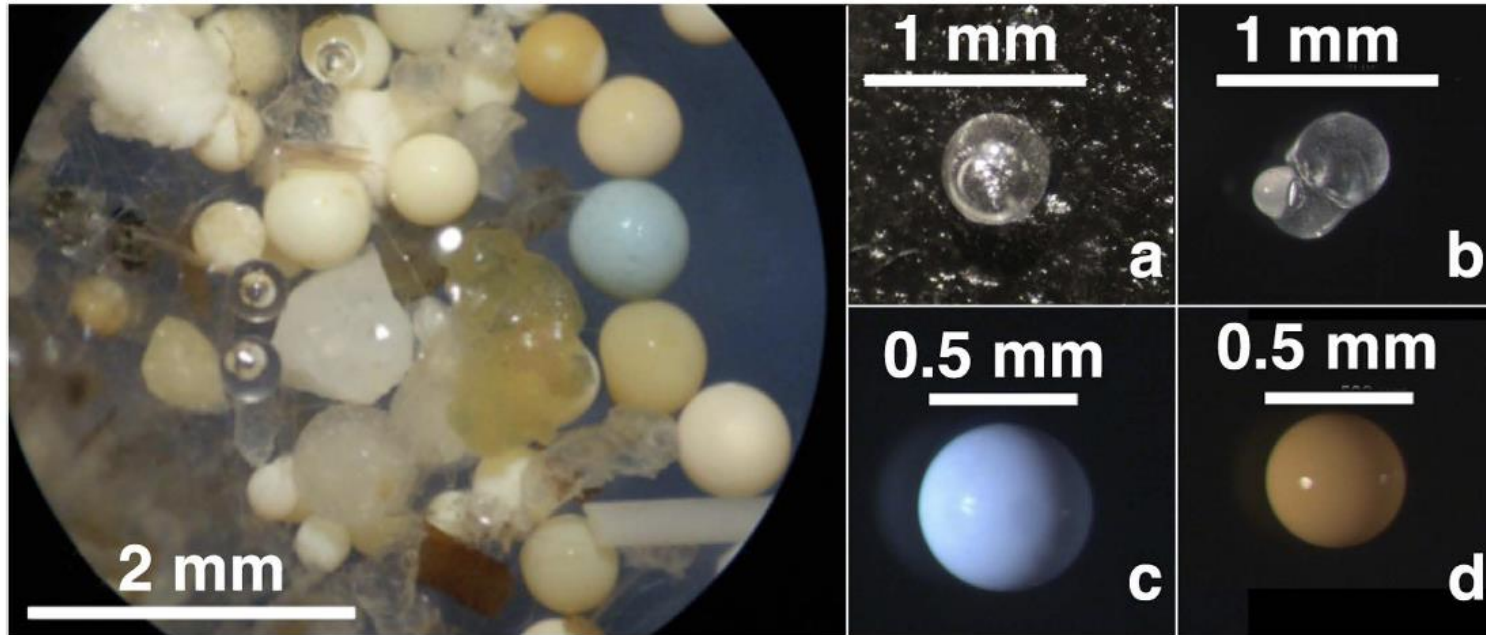
Katherine T. Peter^{a, b}, Skuyler Herzog^c, Zhenyu Tian^{a, b}, Christopher Wu^{a, b}, John E. McCray^c, Katherine Lynch^d, Edward P. Kolodziej^{a, b, e}

- Forcing surface water flow into the streambed
- Engineering the streambed
- Learn from nature (riffle-pool-riffle sequence)





2015: '....there is no microplastics in Swiss rivers...'



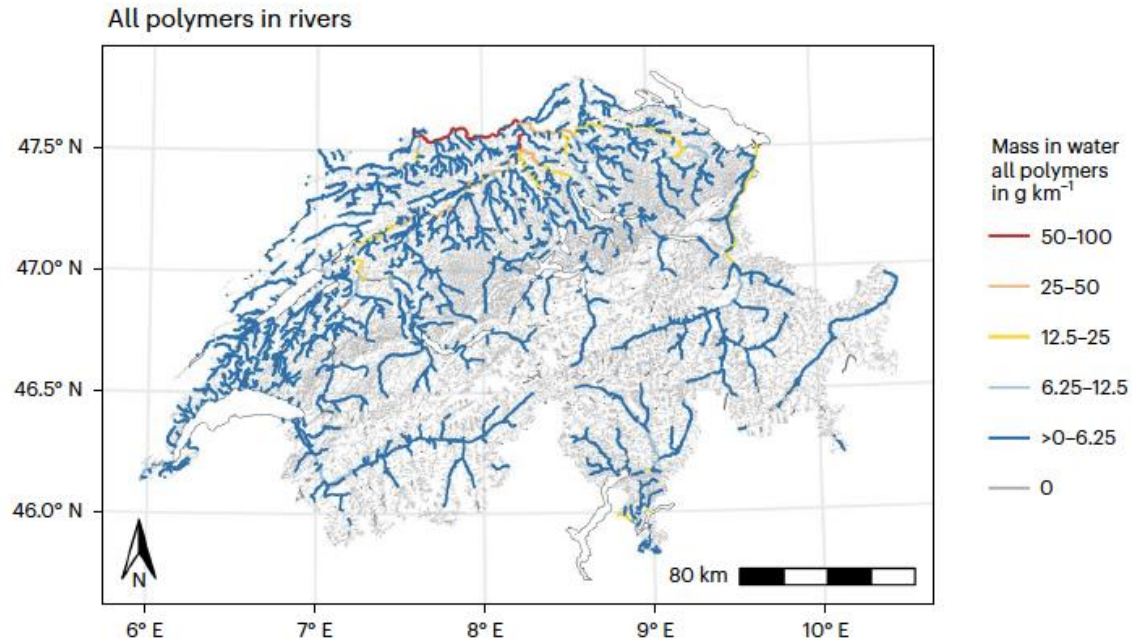
Microplastics profile along the Rhine River

Thomas Mani¹, Armin Hauk², Ulrich Walter² & Patricia Burkhardt-Holm^{1,3}

Figure 2. Typical microplastic categories in the Rhine. Left: Duisburg sample consisting of 65% opaque spherules, further fragments and fibres, bar: 2 mm. (a/b) transparent spherules with gas bubbles, polymethylmethacrylate (Zuilichem), bars: 1 mm; (c/d) opaque spherules, polystyrene (Duisburg, Rees), bars: 500 μm.

Microplastics in rivers

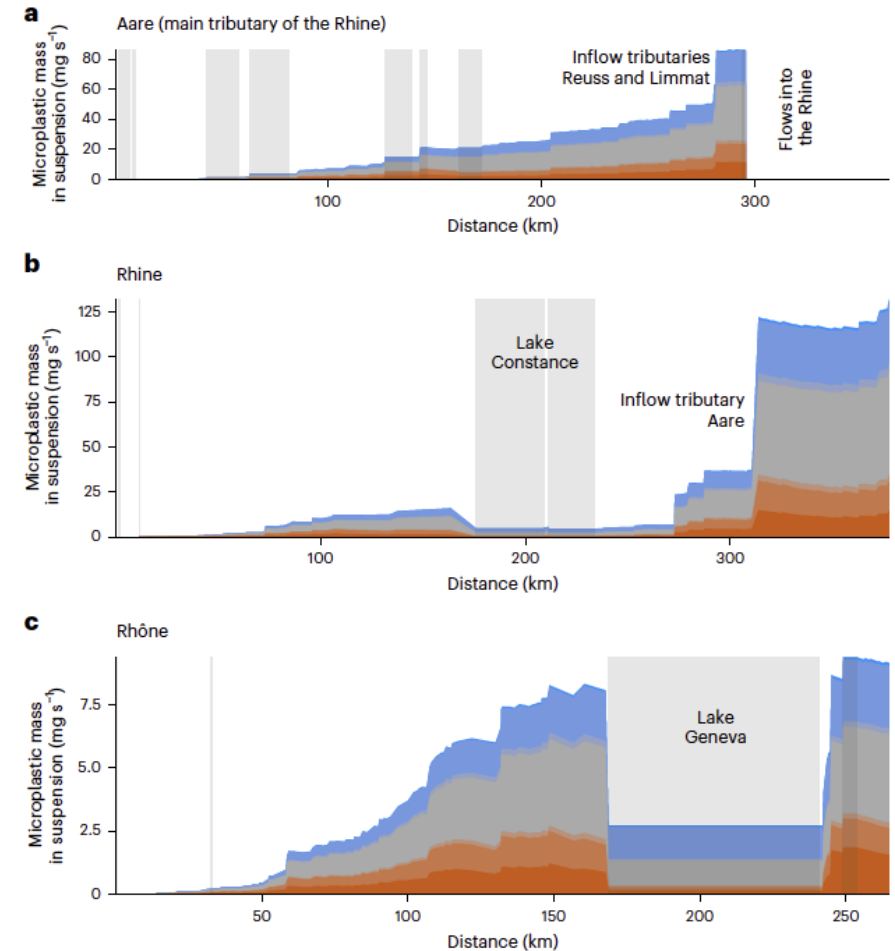
- There is microplastics in Swiss rivers and streams
- Regional/catchment heterogeneity
- Downstream accumulation of MP
- Deposition in lakes and rivers



Predicting microplastic masses in river networks with high spatial resolution at country level

Received: 23 December 2022

David Mennkes & Bernd Nowack



Expanded polystyrene (EPS), polypropylene (PP), low density polyethylene (LDPE), high-density polyethylene (HDPE), polystyrene (PS), polyvinyl chloride (PVC) and polyethylene terephthalate (PET)

Microplastics in rivers

- There is microplastics in Swiss rivers and streams
- Regional/catchment heterogeneity
- Downstream accumulation of MP
- Deposition in lakes and rivers

Modeled scenarios of microplastics loads

- S_0 : no accumulation and sedimentation
- S_{lake} : accumulation and sedimentation in lakes
- S_{all} : accumulation and sedimentation in lakes and rivers

A role for streams and rivers

A role for the hyporheic zone?

Predicting microplastic masses in river networks with high spatial resolution at country level

Received: 23 December 2022

David Mennekes & Bernd Nowack

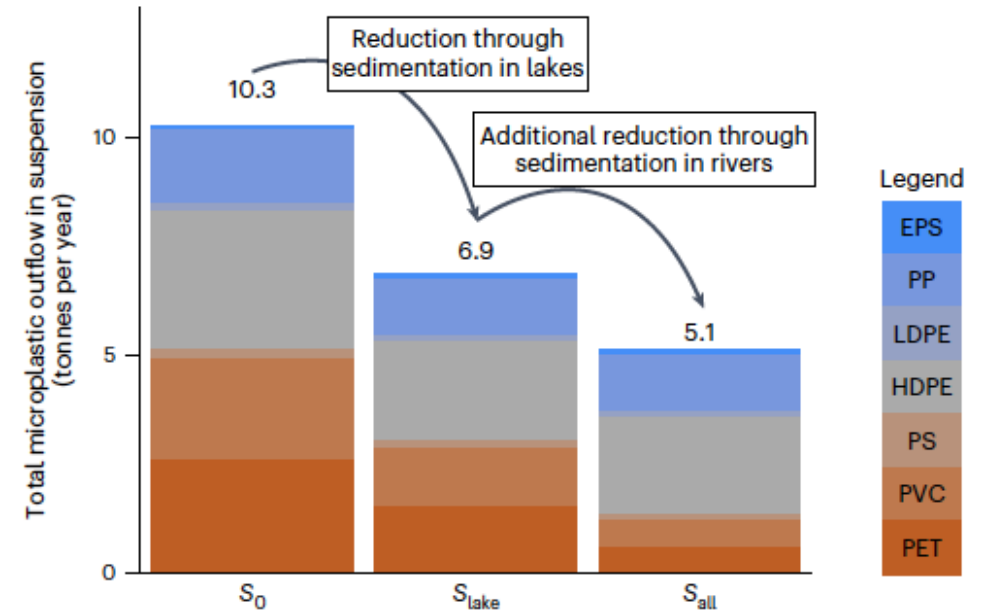


Fig. 2 | Microplastic retention of all analysed polymers differentiated by different colours in entire Switzerland. The scenarios S_0 , S_{lake} and S_{all} are different model runs that consider no sedimentation and accumulation (S_0) sedimentation and accumulation only in lakes (S_{lake}) and sedimentation and accumulation in lakes and rivers (S_{all}). S_0 equals the input emission to the system based on Kawecki and Nowack²⁶. The results represent a steady-state system for the year 2014.

Expanded polystyrene (EPS), polypropylene (PP), lowdensity polyethylene (LDPE), high-density polyethylene (HDPE), polystyrene (PS), polyvinyl chloride (PVC) and polyethylene terephthalate (PET)

Microplastics in rivers and the hyporheic zone

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Microplastic accumulation in riverbed sediment via hyporheic exchange from headwaters to mainstems

Jennifer D. Drummond^{1*}, Uwe Schneidewind¹, Angang Li², Timothy J. Hoellein³, Stefan Krause^{1,4}, Aaron I. Packman²

- Legacy effects
- Fragmentation
- Degradation

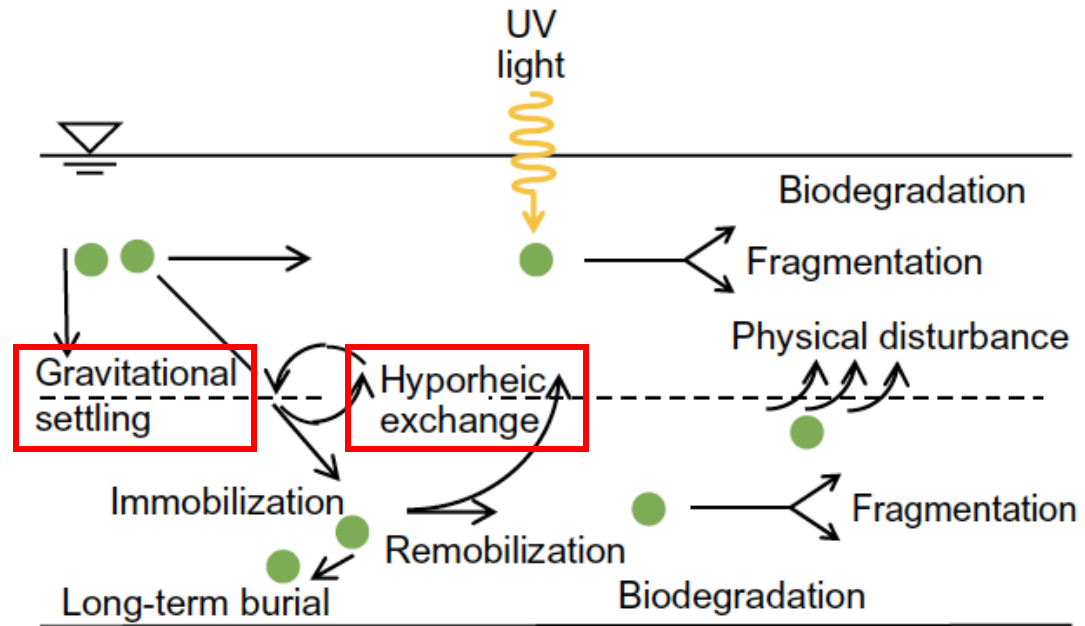


Fig. 1. Processes that control MP accumulation in rivers. Both gravitational settling and hyporheic exchange transport MPs into riverbed sediment, followed by either long-term burial, biodegradation and fragmentation, or remobilization to the water column.

Microplastics in rivers and the hyporheic zone

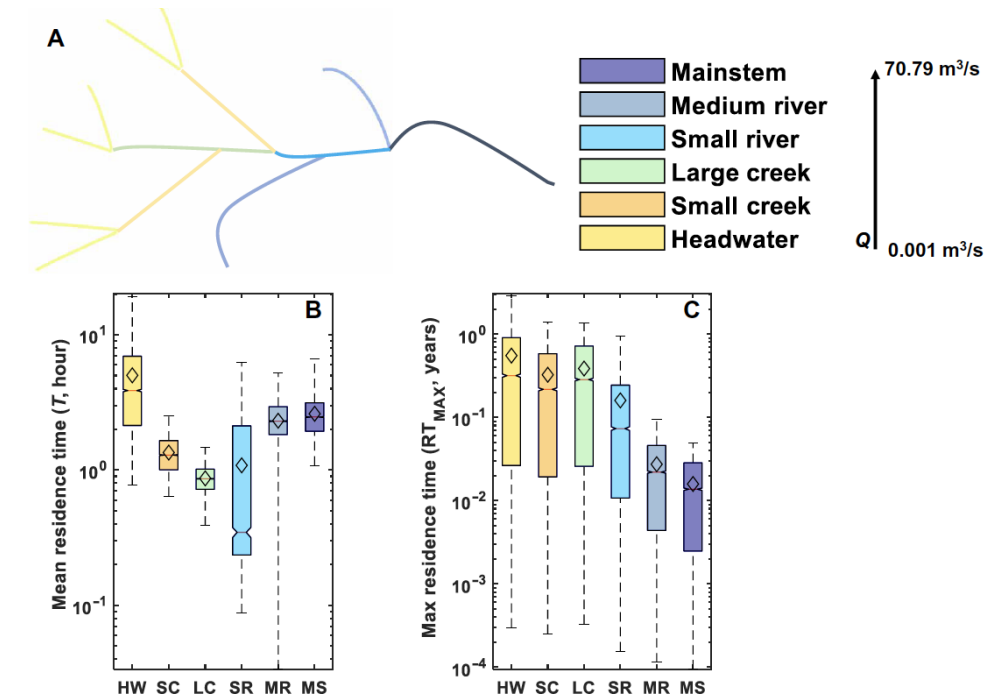
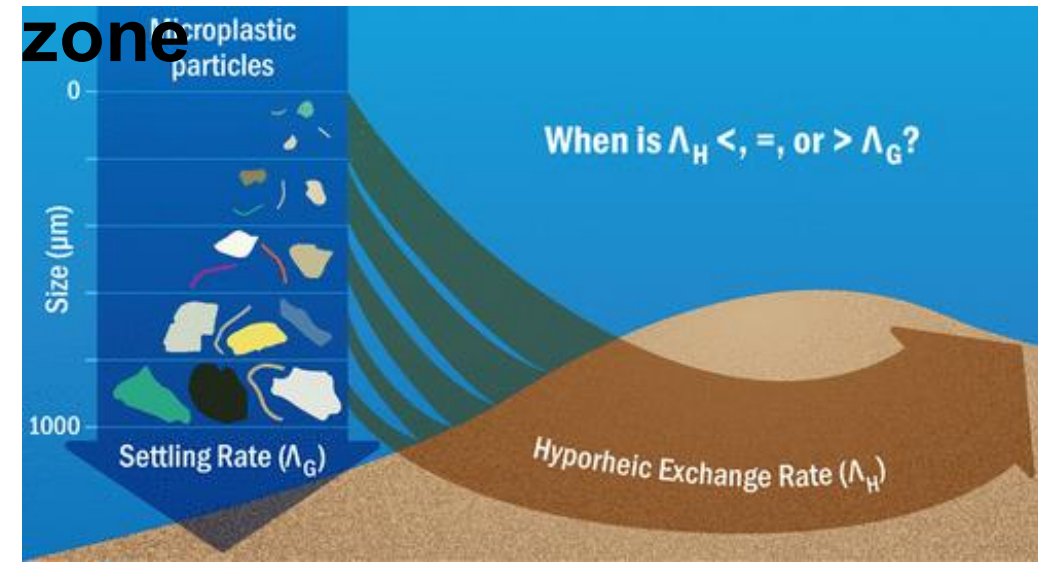
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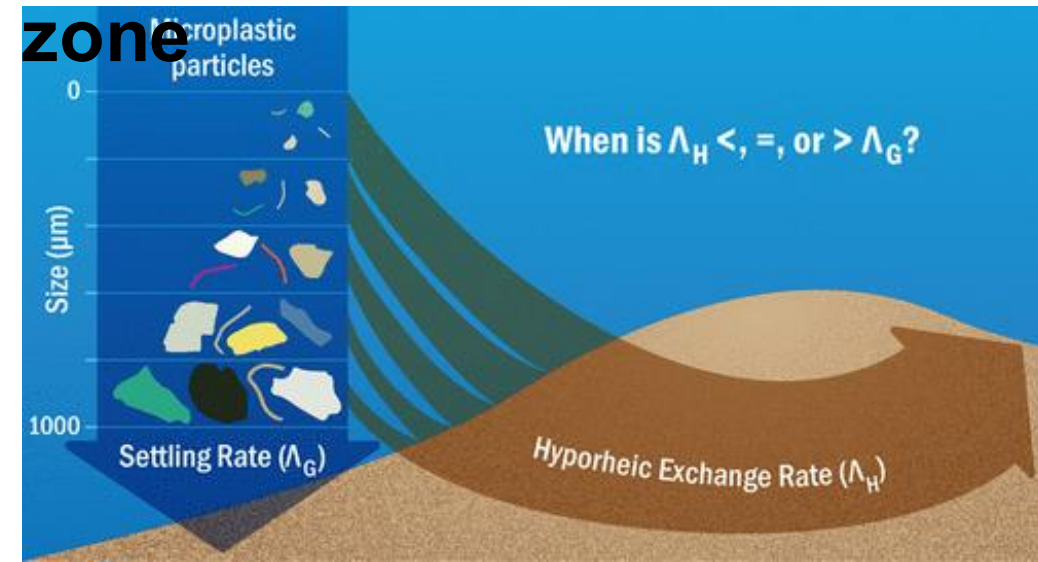
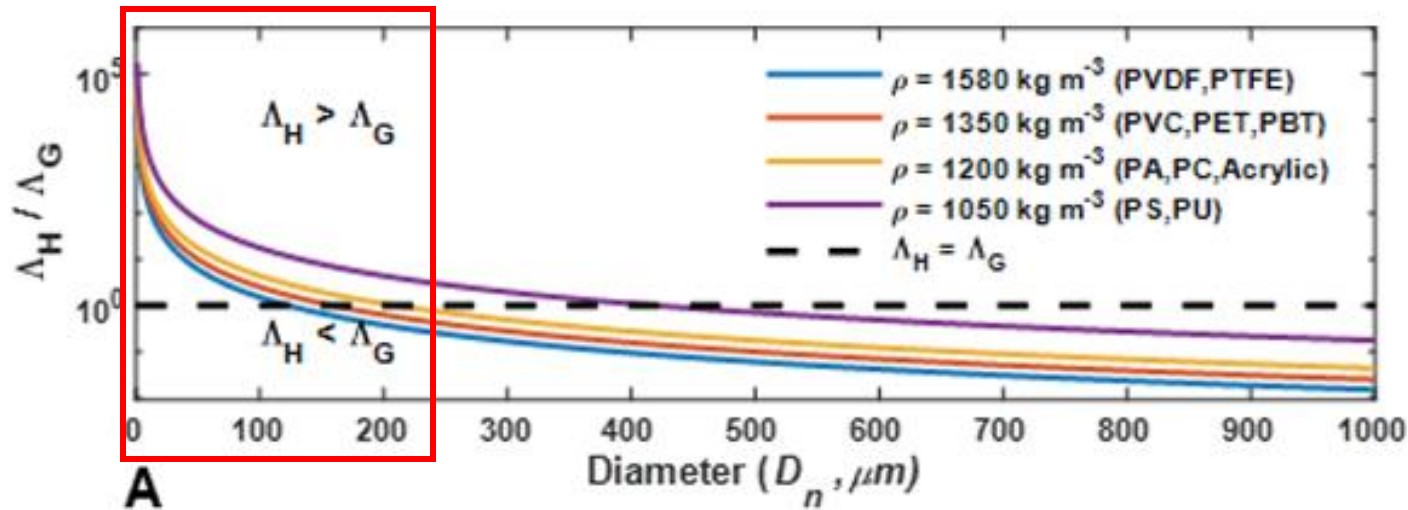
- Simulations indicate that the longest microplastic residence times occur in headwaters, the most abundant stream classification.
- In headwaters, residence times averaged 5 hours/km and increased to 7 years/km during low flow.



Microplastics in rivers and the hyporheic zone

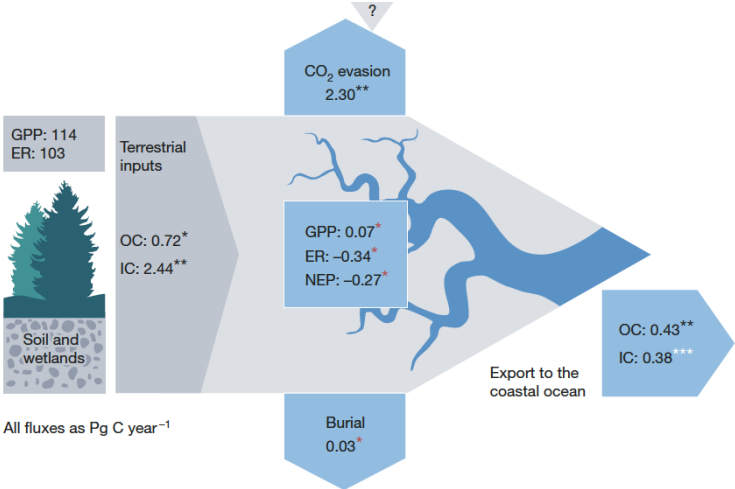
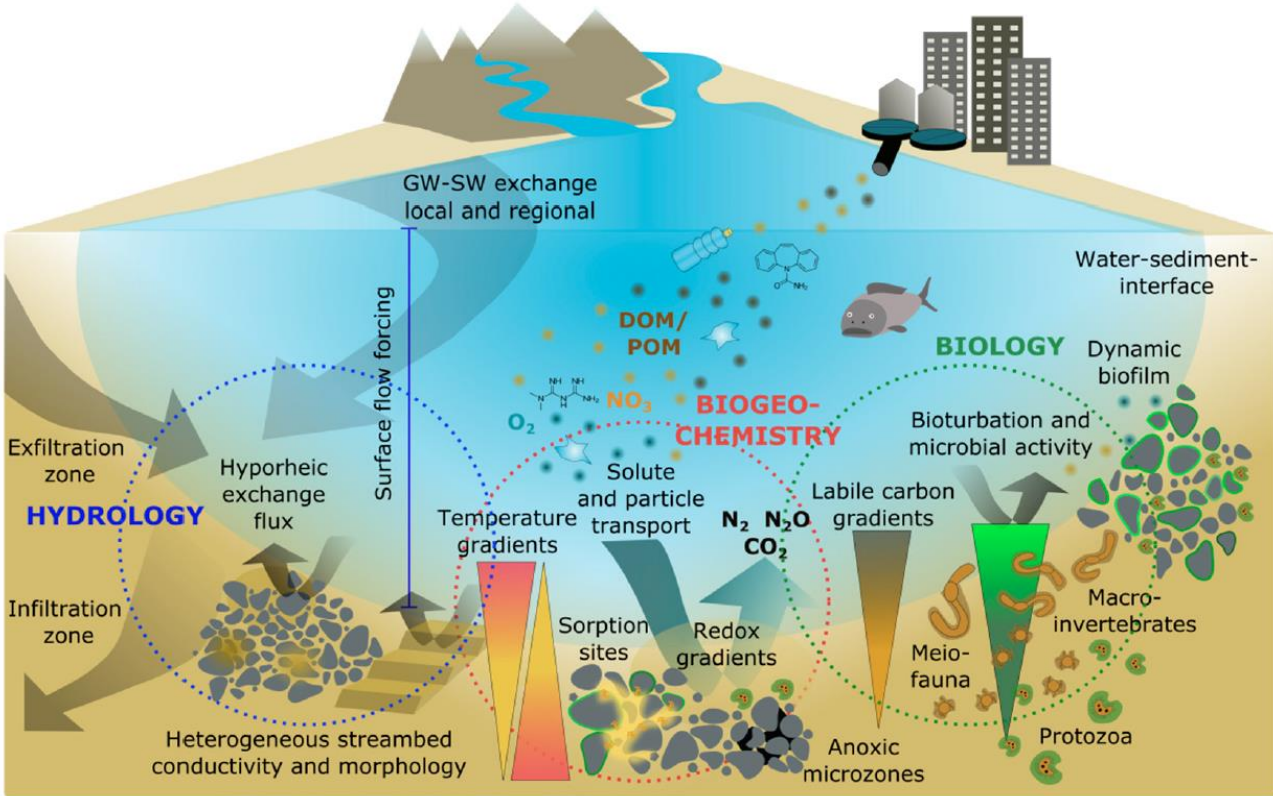
Significance of Hyporheic Exchange for Predicting Microplastic Fate in Rivers

Jennifer D. Drummond,* Holly A. Nel, Aaron I. Packman, and Stefan Krause



- A field experiment showed that 23% of all microplastic combinations have a hyporheic exchange rate that is higher than their settling rate. This fraction was as high as 42% for microplastics composed of low-density polymers, such as polyethylene.
- Hyporheic exchange is important for the transport and fate of particles that are $<100 \mu m$ in diameter, irrespective of polymer type.
- Biofilms increase residence time – through stickiness

Hyporheic processes matter for stream/river ecosystem functioning and health



Hyporheic zone: Contribute to the role streams and rivers play for global biogeochemistry

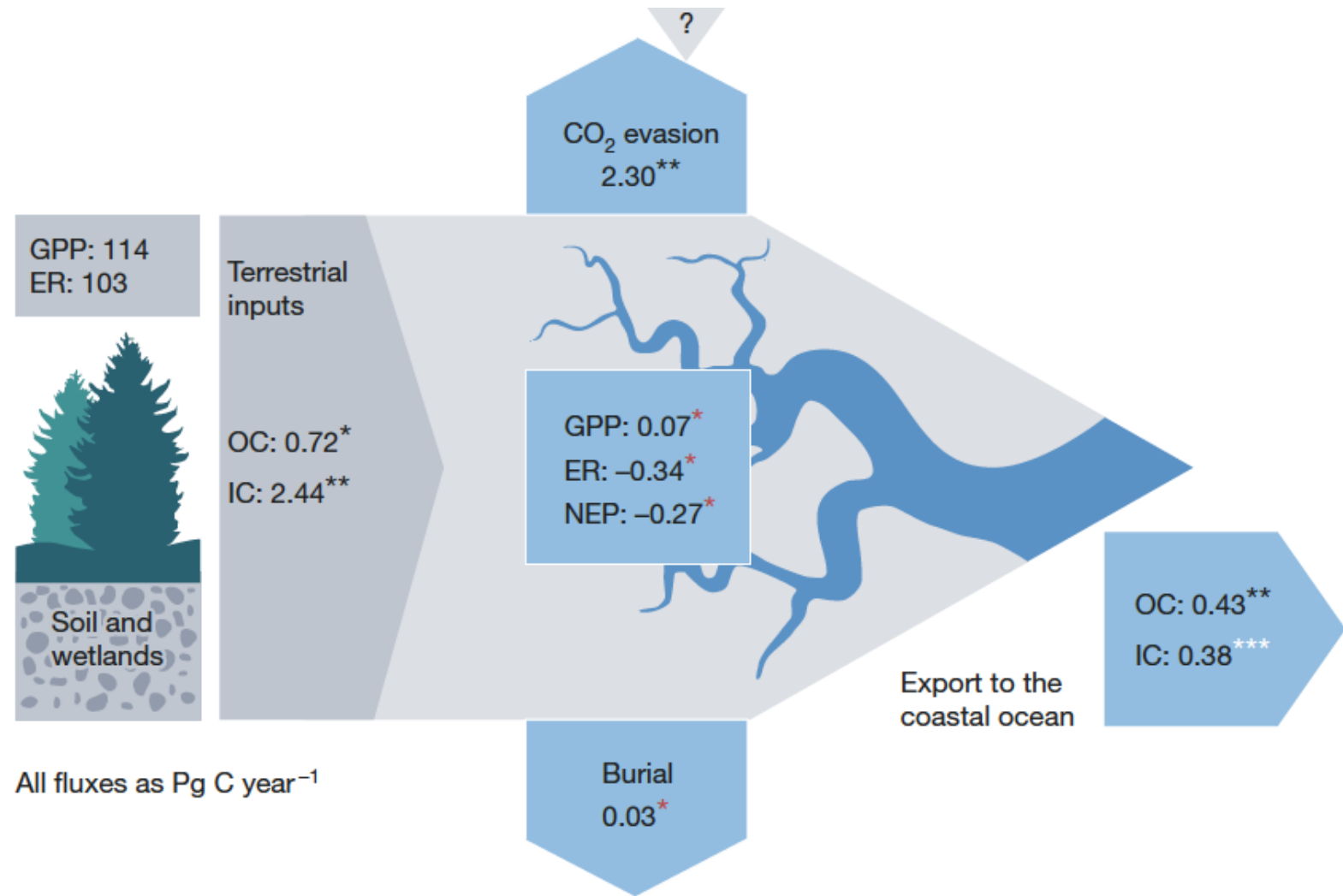
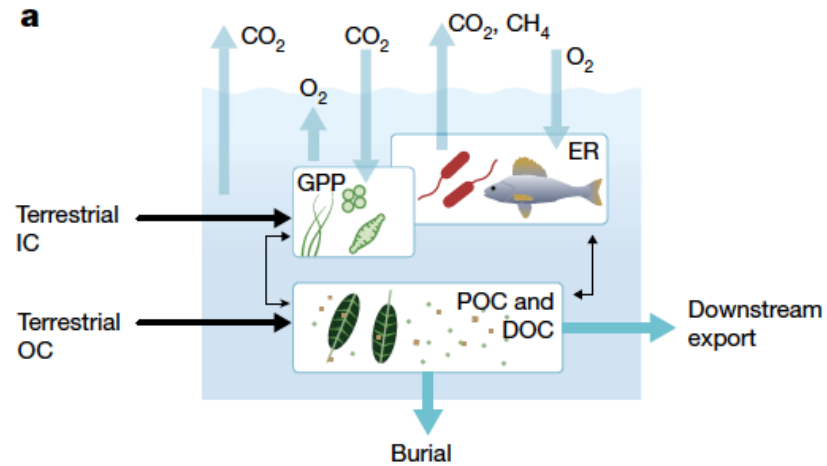
Review

River ecosystem metabolism and carbon biogeochemistry in a changing world

<https://doi.org/10.1038/s41586-022-05500-8> Tom J. Battin^{1,2}, Ronny Lauferwald³, Emily S. Bernhardt⁴, Enrico Bertuzzo⁵, Luis Gómez Gener⁶, Robert O. Hall Jr⁷, Erin R. Hotchkiss⁷, Taylor Maavara⁸, Tamlin M. Pavelsky⁹, Lishan Ran¹⁰, Peter Raymond¹¹, Judith A. Rosenberger^{12,13} & Pierre Regnier¹⁴

Received: 12 March 2021

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Summary

- Streams and rivers are inherent components of the landscape
- Streams and rivers are highly biodiverse
- Biodiversity in streams and rivers at risk
- Anthropogenic alterations across scales (from global change to damming, flow regulation and pollution)
- Environmental heterogeneity critical for biodiversity and ecosystem functions
- Hyporheic processes (physical, chemical and biological) are fundamental for stream and river ecosystem functioning and biogeochemical fluxes