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Unravelling large-scale patterns and drivers of biodiversity in dry rivers

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More than half of the world's rivers dry up periodically, but our understanding of the biological communities in dry riverbeds remains limited. Specifically, the roles of dispersal, environmental filtering and biotic interactions in driving biodiversity in dry rivers are poorly understood. Here, we conduct a large-scale coordinated survey of patterns and drivers of biodiversity in dry riverbeds. We focus on eight major taxa, including microorganisms, invertebrates and plants: Algae, Archaea, Bacteria, Fungi, Protozoa, Arthropods, Nematodes and Streptophyta. We use environmental DNA metabarcoding to assess biodiversity in dry sediments collected over a 1-year period from 84 non-perennial rivers across 19 countries on four continents. Both direct factors, such as nutrient and carbon availability, and indirect factors such as climate influence the local biodiversity of most taxa. Limited resource availability and prolonged dry phases favor oligotrophic microbial taxa. Co-variation among taxa, particularly Bacteria, Fungi, Algae and Protozoa, explain more spatial variation in community composition than dispersal or environmental gradients. This finding suggests that biotic interactions or unmeasured ecological and evolutionary factors may strongly influence communities during dry phases, altering biodiversity responses to global changes.

Anthropogenic activities are causing dramatic declines in the biodiversity of river ecosystems^{1,2}. Assessments of river biodiversity have primarily focused on perennial rivers^{2–4}, or flowing phases in non-perennial rivers (NPRs)^{5,6}, reporting significant population declines and species losses across taxa including insects, fish and birds. NPRs, which naturally experience dry phases, constitute more than half of the global river network length^{7,8} and are increasing in extent due to climate change and escalating demands for freshwater⁹. Understanding biodiversity patterns and the underlying assembly rules that govern community establishment during dry phases is crucial to anticipate the response of NPR biodiversity and ecosystem functioning to global change, including changing patterns of river drying.

Spatial and temporal shifts between wet and dry states in NPR channels generate complex and dynamic mosaics of wet and dry habitats¹⁰. Extended dry phases generally reduce the local biodiversity (i.e., alpha-diversity) of aquatic taxa (e.g., invertebrates, fishes) but increase compositional variation among communities (i.e., beta-diversity), due to spatial co-occurrence of communities in dry and wet

habitats, and species turnover during wet–dry cycles¹¹. During dry phases, riverbeds provide habitat and food for diverse amphibious and terrestrial organisms^{12,13}. However, while understanding of the aquatic biota present during flowing phases is increasing^{6,11,14}, knowledge of dry-phase communities remains limited (but see ref. 12), even though these communities control major biogeochemical cycles through organic matter decomposition, nutrient cycling and greenhouse gas emissions^{15–17}.

Furthermore, how biotic interactions, dispersal and environmental filtering influence dry-phase biodiversity and community assembly is not well understood^{18,19}. In terms of biotic interactions, some protozoans may be more resistant to dry phases than macroinvertebrates, which may increase protozoan control on bacterial populations²⁰. Regarding dispersal, microbial communities are also typically less constrained by dispersal than macroorganisms²¹. As such, the dendritic structure of river networks and the unidirectional passive transport of organisms in flowing water could generate patterns of decreasing alpha-diversity from headwaters to downstream reaches

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and high beta-diversity among headwaters²². This pattern particularly applies to microbial diversity, but also holds for active dispersers such as fish and aquatic insects with flying adult stages^{23–25}. Drying temporarily fragments river networks, disrupting upstream-downstream linkages, with consequences for dispersal and thus community assembly²⁶.

Drying may act as a strong environmental filter on riverbed communities by increasing osmotic stress and reducing substrate diffusion²⁷. Organic carbon and inorganic nutrient availability is also lower in dry riverbeds than in soils or the sediments of perennial riverbeds¹⁷, which may constrain dry-phase biodiversity²⁰. Beyond taxonomic changes, dry conditions may select for specific biological traits that parallel those of soil organisms, which inhabit environmental conditions shared with dry riverbeds²⁸. Microorganisms have been grouped according to ecological strategies that reflect traits relating to growth, competition, and resistance to environmental stress, partly analogous to the r/K strategies used to classify higher organisms²⁹. Dry conditions in soils select for oligotrophic microorganisms (including some Bacteria and Fungi), which are characterized by slow growth, high investment in extracellular enzyme production for resource acquisition, and high resistance to environmental stress, whereas copiotrophic microorganisms grow quickly, thrive in resource-rich environments and show low resistance to environmental stress^{30,31}. Such increases in the relative abundance of oligotrophic Bacteria (e.g., Actinobacteria, Alphaproteobacteria) or Fungi (e.g., Basidiomycota) also occur in response to experimental sediment desiccation³². In other taxa, such as Algae, resistance to dry conditions is facilitated by dormant spores and protective carotenoids³³, whereas Nematoda often undergoes anhydrobiosis to survive dry phases³⁴. In addition, Arthropoda have a wide range of adaptations conferring resistance or resilience to dry conditions³⁵. Dry phases should thus support organisms with traits reflecting the ability to cope with these harsh environmental conditions.

Previous efforts to quantify the dry-phase biodiversity of NPRs have been restricted, both geographically and taxonomically^{36–38}, with large-scale coordinated surveys needed to fill this gap. Environmental DNA (eDNA) metabarcoding is an efficient approach in large standardized surveys, because it allows the simultaneous identification of multiple taxa^{39–41}. Here, we present the first large-scale assessment of NPR biodiversity during dry phases, using metabarcoding of sediment eDNA from 84 dry rivers in 19 countries on four continents. Our aim was to characterize the alpha- and beta-diversity of dry-riverbed communities and to identify their major potential drivers. We analyzed the diversity of eight major taxa (Algae, Archaea, Bacteria, Fungi, Protozoa, Arthropoda, Nematoda and Streptophyta), and estimated the relative abundance of copiotrophic and oligotrophic microorganisms. We investigated differences in community composition between continents and climate classes, then used random forest modeling and correlation networks inferred from graphical models to assess the relative contribution of potential abiotic and biotic drivers of biodiversity patterns. Our first hypothesis was that the availability of key resources, i.e., organic carbon and inorganic nutrients, is positively related to the taxonomic richness (i.e., alpha-diversity) of dry-riverbed communities, whereas limited water availability, caused by low precipitation and long dry-phase durations, decreases richness²⁰. We also predicted that resource limitation promotes oligotrophic microorganisms adapted to coping with the harsh conditions in dry sediments³⁰. Our second hypothesis was that spatial community variation (i.e., beta-diversity) in dry riverbeds is primarily controlled by environmental filtering and to a lesser extent by biotic interactions^{20,33,35}.

In this work, we investigate the potential drivers of microbial, invertebrate, and plant biodiversity in dry riverbeds. Our findings indicate that variables related to resource and water availability are important predictors of alpha-diversity during dry phases.

Additionally, our results suggest that biotic interactions may be more important to the assembly of dry-riverbed communities than dispersal or environmental filters.

Results

The composition of dry-riverbed communities

The 84 sediment samples were collected in regions spanning the main five Köppen climate classes, with most collected in temperate and arid regions (tropical $n=2$, arid $n=14$, temperate $n=66$, continental $n=1$, polar $n=1$; Fig. 1). Our sampling design covered a wide gradient of physicochemical conditions and land uses (Table S1) and included river channels up to 11 m wide (mean \pm sd = 3.5 ± 2.4 m), in many cases with adjacent riparian vegetation ($64 \pm 33\%$). Sampling sites were predominantly in headwater streams (Strahler order 1 = 38%, 2 = 25%, 3 = 24%, 4 = 8%, 5 = 4%, and 6 = 1%), and at a mean \pm sd elevation of 436 ± 469 m (range 24–2852 m). Sediment organic carbon content ranged from 0.1–8.5% ($1.3 \pm 1.7\%$) (Table S1). The duration of the dry-phase preceding sample collection ranged from 7–800 days.

eDNA metabarcoding identified 131 operational taxonomic units (OTUs) of Algae, 82 of Archaea, 2035 of Bacteria, 744 of Fungi, 520 of Protozoa, 158 of Arthropoda, 93 of Nematoda and 51 of Streptophyta. Actinobacteria were the most common phylum detected with the 16S marker, followed by Proteobacteria and Bacteroidetes (Fig. 2). Within the Proteobacteria, the most abundant classes were Alphaproteobacteria (mean \pm sd = $11.5 \pm 6.4\%$ of the total number of reads, $n=84$), Gammaproteobacteria ($8.6 \pm 9.1\%$) and Betaproteobacteria ($4.6 \pm 4.5\%$). Within the Eukaryota, the most abundant phyla detected with the 18S marker corresponded to Fungi ($49 \pm 22\%$, $n=76$), with Ascomycota ($26 \pm 19\%$) and Basidiomycota ($11 \pm 13\%$) being the most common phyla (Fig. 3). OTUs for Algae and Protozoa contributed on average 5% and 14%, respectively. Twelve metazoan phyla were detected, with the highest relative abundances corresponding to Arthropoda ($8 \pm 12\%$) followed by Nematoda ($3 \pm 4\%$). Sequences assigned to Arthropoda included Collembola ($3 \pm 7\%$), Ostracoda ($2 \pm 6\%$), and Arachnida ($2 \pm 3\%$, corresponding mainly to mites). Around 4% of the reads corresponded to Streptophyta.

Patterns and drivers of alpha-diversity in dry riverbeds

Bacteria had the highest OTU richness per sample based on the Chao1 estimator (mean \pm sd = 375 ± 135 ; min–max = 59–695, Fig. S1), followed by Fungi (101 ± 38 ; 22–200, Fig. S2), Protozoa (70 ± 40 ; 5–187, Fig. S3), Algae (13 ± 9 ; 1–58, Fig. S4), Nematoda (10 ± 8 ; 0–36, Fig. S5), Arthropoda (7 ± 6 ; 0–27, Fig. S6), Archaea (7 ± 5 ; 1–38, Fig. S7) and Streptophyta (4 ± 2 ; 0–14, Fig. S8). Random forest models explained 5.0–34.7% of the total variance in OTU richness among the eight taxa. Model performance was highest for Nematoda (34.7% of the total variance in OTU richness explained); intermediate for Streptophyta (26%), Bacteria (22.7%), Algae (18.7%), Protozoa (17.3%), Fungi (14%) and Archaea (13.7%); and lowest for Arthropoda (5%).

Mean annual temperature and precipitation were important predictors of variation in OTU richness for all taxa except Bacteria (Table 1). OTU richness peaked at mean annual temperatures between 10 °C and 20 °C for Archaea (Fig. S15), Fungi (Fig. S10), and Protozoa (Fig. S11). OTU richness of Nematoda (Fig. S13) and Streptophyta (Fig. S16) decreased at mean temperatures >10 °C, whereas the richness of Algae decreased above 15 °C (Fig. S12). OTU richness of Algae (Fig. S12), Arthropoda (Fig. S14), and Streptophyta (Fig. S16) peaked at a mean annual precipitation of 500–1000 mm, and the richness of Nematoda increased with precipitation (Fig. S13). Dry-phase duration was negatively correlated with the OTU richness of Archaea and Algae, which declined sharply within 100 days of dry-phase onset (Figs. S15 and S12). The OTU richness of Fungi, Protozoa, and Arthropoda was higher at dry-phase durations ≤ 100 days and slightly decreased or plateaued when dry phases were longer (Figs. S10, S11, and S14).

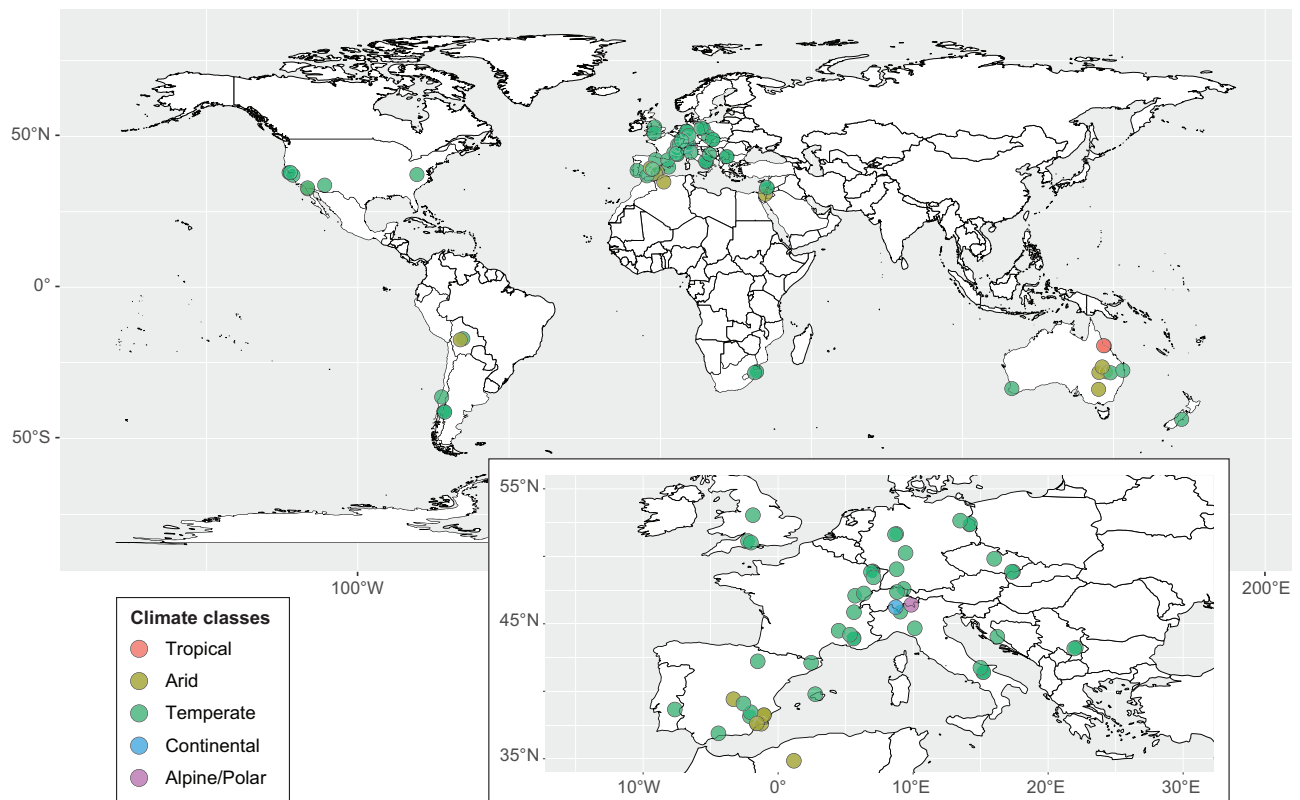


Fig. 1 | Location of 84 dry-riverbed sampling sites and their Köppen climate class. The inset illustrates site locations within the most densely sampled area.

Most variables related to resource availability in sediments (i.e., organic carbon content and soluble reactive phosphorus [SRP], but not dissolved inorganic nitrogen [DIN] concentrations) were important predictors of the variation in OTU richness for most taxa. Carbon content was positively related to the OTU richness of heterotrophic organisms (e.g., Protozoa and Arthropoda) but was a poor predictor of the richness of autotrophic groups, i.e., Algae and Streptophyta (Table 1, Figs. S11 and S14). The OTU richness of Archaea, Bacteria, Fungi, Protozoa, and Arthropoda (Figs. S15, S9, S10 and S14) sharply increased and then plateaued at carbon contents >1%. Bacteria and Nematoda OTU richness increased sharply with SRP and plateaued at concentrations $>1 \mu\text{g g}^{-1}$ sediment dry weight (Figs. S9 and S13), whereas Archaea richness decreased with SRP (Fig. S15). OTU richness of Bacteria was positively related to pH (Fig. S9), whereas the richness of Archaea, Algae, Protozoa, and Streptophyta sharply increased at pH >6.5 and then plateaued (Archaea and Streptophyta; Figs. S15, S12, S11, and S16) or decreased at pH >7.5 (Protozoa and Algae; Figs. S11–S12).

The OTU richness of Nematoda (Fig. S13) increased with riparian cover whereas Fungi and Protozoa richness decreased at >50% cover (Figs. S10, S11). The OTU richness of most taxa was weakly correlated with variables related to river size (i.e., river width and catchment area). Nematoda and Streptophyta OTU richness were higher in the smallest catchments and Archaea OTU richness peaked at river widths between 2–6 m. Land use variables (percentage of forest or urban land cover in the catchment) were never selected as predictors of OTU richness (Table 1).

Variables selected in random forest models explained 29% and 8% of the variation in the bacterial and fungal copiotrophic:oligotrophic ratios, respectively. The relative abundance of copiotrophic Bacteria increased with resource (e.g., SRP) availability and decreased with dry-phase duration and temperature (Fig. 4). The relative abundance of oligotrophic Fungi (i.e., Basidiomycota) increased with increasing organic carbon content, C:N ratio and riparian cover (Fig. S17).

Patterns and drivers of beta-diversity in dry riverbed sediments

Community composition differed between Eurasia and Oceania for all taxa except Arthropoda (PERMANOVA, $p < 0.05$, Figs. S18–21 and S23–25), but only in temperate climates for Nematoda (Fig. S22). Community composition differed between Eurasia and America for Bacteria, Protozoa, and Streptophyta ($p < 0.05$, Figs. S18, S20, and S25), but only in temperate climates for Nematoda (Fig. S22). The composition of Bacteria, Algae, and Arthropoda communities differed between Oceania and America ($p < 0.05$, Figs. S18, S21, and S23). Community composition differed between temperate and arid climates for Bacteria, Fungi, and Protozoa ($p < 0.05$, Figs. S18–20), but only in Oceania and Eurasia for Nematoda (Fig. S22).

We identified associations between the beta-diversity of each taxon using a partial correlation network inferred with the graphical lasso method (Fig. 5). The beta-diversity of Fungi and Bacteria was strongly associated with the beta-diversity of other taxa (e.g., Protozoa, Algae, Nematoda) in terms of both strength (weighted degree values of 0.82 and 0.77, respectively) and the number of links with other taxa (degree value of 5). The highest partial correlations were observed between Fungi and Bacteria. Protozoa (weighted degree value of 0.69, degree value of 5) and Algae (0.52, 5) were also strongly associated with other taxa, in particular Fungi and Bacteria. The beta-diversity of Protozoa had a particularly strong positive correlation with the beta-diversity of Algae and Fungi and, to a lesser extent, Archaea (Fig. 5). A strong relationship was also observed between Nematoda and Bacteria. The beta-diversity of Arthropoda was not correlated with that of other taxa.

The Euclidean spatial distance between sampling sites, which represents an indirect measure of dispersal limitation, was weakly positively correlated with the beta-diversity of Bacteria and Streptophyta. The rate of change in environmental conditions (i.e., climatic, physicochemical, and land-use variables) was a poor predictor of the beta-diversity for any taxon with few exceptions: the beta-diversity of Bacteria was correlated with temperature change and to a lesser extent

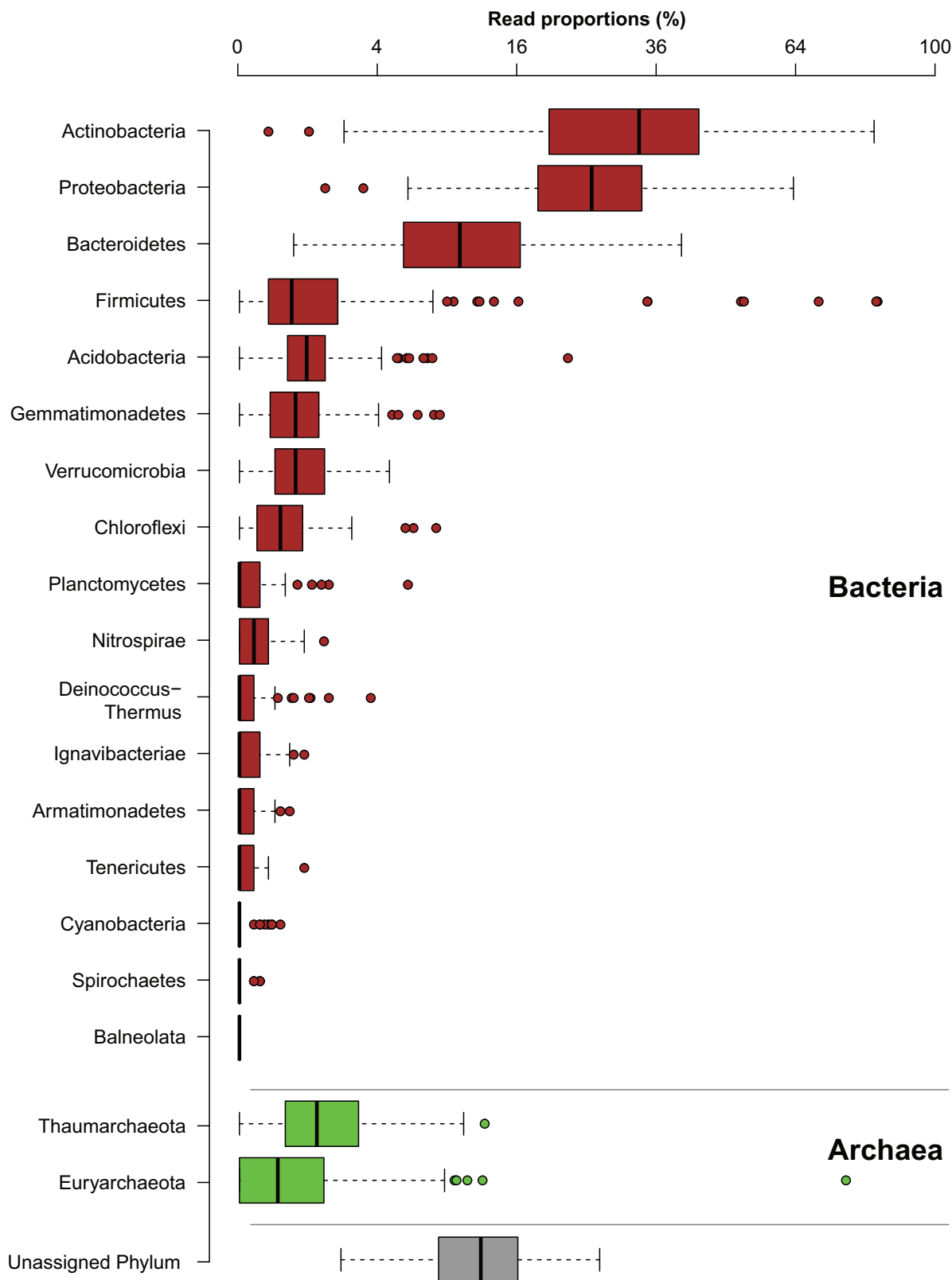


Fig. 2 | Composition of Bacteria and Archaea communities in dry riverbed sediments (n = 84). Read proportions (square root scale) correspond to the relative abundance of each taxon per sample and were estimated using the 16S marker dataset rarefied to 2311 reads per sample. The vertical bold line within the box represents the median. The upper and lower limits of the box represent the 75th

and 25th percentiles. Horizontal dotted lines indicate the range of observed values within 1.5× the interquartile range from the 75th and 25th percentiles. Values outside this range were considered outliers and are indicated as points. Source data are provided as a Source Data file.

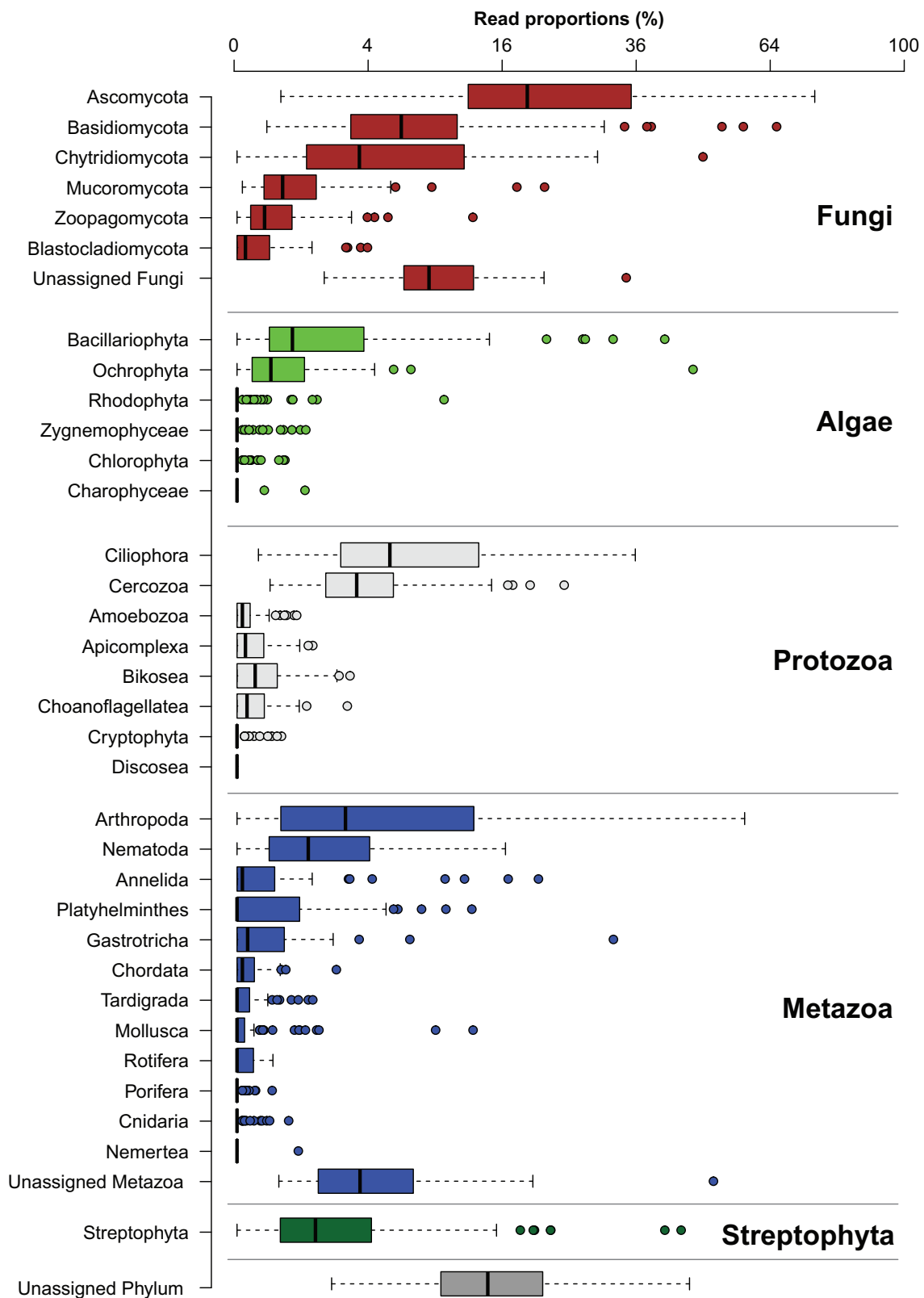


Fig. 3 | Composition of eukaryotic communities in dry riverbed sediments ($n = 76$). Read proportions (square root scale) correspond to the relative abundances of each taxon per sample and were estimated using the 18S marker dataset

rarefied to 15624 reads per sample. Further details are provided in the Fig. 2 legend. Source data are provided as a Source Data file.

Table 1 | Contribution of physicochemical, land-use, and climatic variables to variation in operational taxonomic unit (OTU) richness in dry riverbed communities

Predictor	Archaea (% exp. = 13.7; n = 84)	Bacteria (% exp. = 22.7; n = 84)	Fungi (% exp. = 14.3; n = 76)	Algae (% exp. = 18.7; n = 76)	Protozoa (% exp. = 17.3; n = 76)	Nematoda (% exp. = 34.7; n = 76)	Arthropoda (% exp. = 5.0; n = 76)	Streptophyta (% exp. = 26.0; n = 76)
<i>Environmental variables</i>	%IncMSE	%IncMSE	%IncMSE	%IncMSE	%IncMSE	%IncMSE	%IncMSE	%IncMSE
Carbon content	19.2	21.4	19.9	-	22.2	-	21.1	-
Carbon:Nitrogen ratio	-	13.7	-	-	-	-	-	-
Dissolved inorganic nitrogen	-	-	-	-	-	-	-	-
Soluble reactive phosphorus	13.0	28.5	-	-	-	19.9	-	-
pH	22.4	21.4	-	10.8	18.4	-	-	29.7
Mean sediment particle size	-	-	-	-	-	-	10.9	-
Catchment area	-	-	-	-	-	26.7	-	25.2
River width	16.1	-	-	-	-	-	-	-
Riparian cover	-	-	20.7	-	18.0	24.7	-	-
Percentage forest	-	-	-	-	-	-	-	-
Percentage urban	-	-	-	-	-	-	-	-
Dry-phase duration	16.7	-	16.5	28.5	13.9	-	14.0	-
<i>Climatic variables</i>								
Mean annual temperature	14.6	-	29.7	35.5	29.2	45.8	-	28.8
Mean annual precipitation	14.7	-	-	27.9	-	22.1	4.8	29.3

% exp. the percentage of explained variation in OTU richness, n the number of analyzed samples, %IncMSE the increase in the mean-square error of the predictions when the variable is randomly permuted, indicating the importance of predictors in a random forest model, values are proportional to variable importance.

with SRP and river width, and that of Fungi and Archaea was correlated with catchment area and SRP, respectively (Fig. 5).

Discussion

Previous eDNA-based studies have revealed high microbial and metazoan diversity in perennial rivers^{42–44}. However, although the contribution of dry riverbeds to the ecosystem functioning and services of NPRs is increasingly recognized^{15–17}, dry-riverbed biodiversity remains poorly characterized relative to perennial rivers. Our eDNA metabarcoding analyses of samples collected during a large-scale coordinated survey reveal patterns and potential drivers of microbial, invertebrate, and plant biodiversity in dry riverbeds. Assuming adequate representation of the major abiotic variables, the strong linkages observed among the beta-diversity of Bacteria, Fungi, Algae, Protozoa and Nematoda suggest that biotic interactions may be more important to the assembly of dry-riverbed communities than dispersal or environmental filters.

Resource availability and climate as drivers of OTU richness in dry riverbeds

In line with our first hypothesis, variables related to resource availability (organic carbon content or soluble reactive phosphorus [SRP] concentrations) and water availability (precipitation and dry-phase duration) were important predictors of OTU richness in dry NPR sediments. For most taxa, climatic variables were the main predictors of OTU richness, whereas Bacteria were primarily influenced by resource availability. The increase in the OTU richness of heterotrophic organisms with the availability of organic carbon aligns with its positive influence on microbial diversity in marine sediments⁴⁵ and increases in soil biodiversity along plant productivity gradients⁴⁶. Conversion of carbon to microbial biomass facilitates energy transfer to higher trophic levels (e.g., Nematoda, Protozoa, Arthropoda), although many species within these taxa also consume dead organic

matter. The saturating (as opposed to unimodal) relationship of OTU richness with organic carbon availability suggests that competitive exclusion might not strongly affect the alpha-diversity of heterotrophic communities in dry riverbeds, mirroring observations made in soils⁴⁶.

Nutrient limitation, particularly by phosphorus, also appeared to influence the biodiversity in dry riverbeds, as indicated by a sharp increase in OTU richness as sediment SRP concentrations increased. This suggests that dry-phase biodiversity might be constrained by resource availability, at least in oligotrophic conditions. Furthermore, our results indicate that heterotrophic microbial communities might be more limited by carbon or phosphorus than by nitrogen availability⁴⁷. However, although algal richness is typically constrained by inorganic nutrients in freshwaters⁴⁸, nutrient availability had less influence on the OTU richness of Algae and Streptophyta in dry riverbeds than climatic variables. The rapid decrease in algal OTU richness as dry-phase durations increased reflects biodiversity loss as taxon-specific desiccation-tolerance thresholds were sequentially surpassed³³. In contrast, the OTU richness of Arthropoda, Fungi, and Protozoa increased during dry phases of moderate duration (i.e., up to 100 days), which may reflect the colonization of terrestrial and semi-aquatic taxa from riparian habitats and their contribution to dry-riverbed communities⁴⁹.

Community composition of dry riverbeds revealed by eDNA metabarcoding

Our analyses indicate that specific ecological adaptations to dry conditions and low-resource environments influence bacterial community assembly in dry riverbeds. Increased resource availability in the form of SRP favored copiotrophic bacteria, whereas prolonged dry phases, organic matter recalcitrance (indicated by high C:N ratios) and increased catchment-scale forest cover (corresponding to a decrease in agricultural land cover) caused a shift towards taxa with an

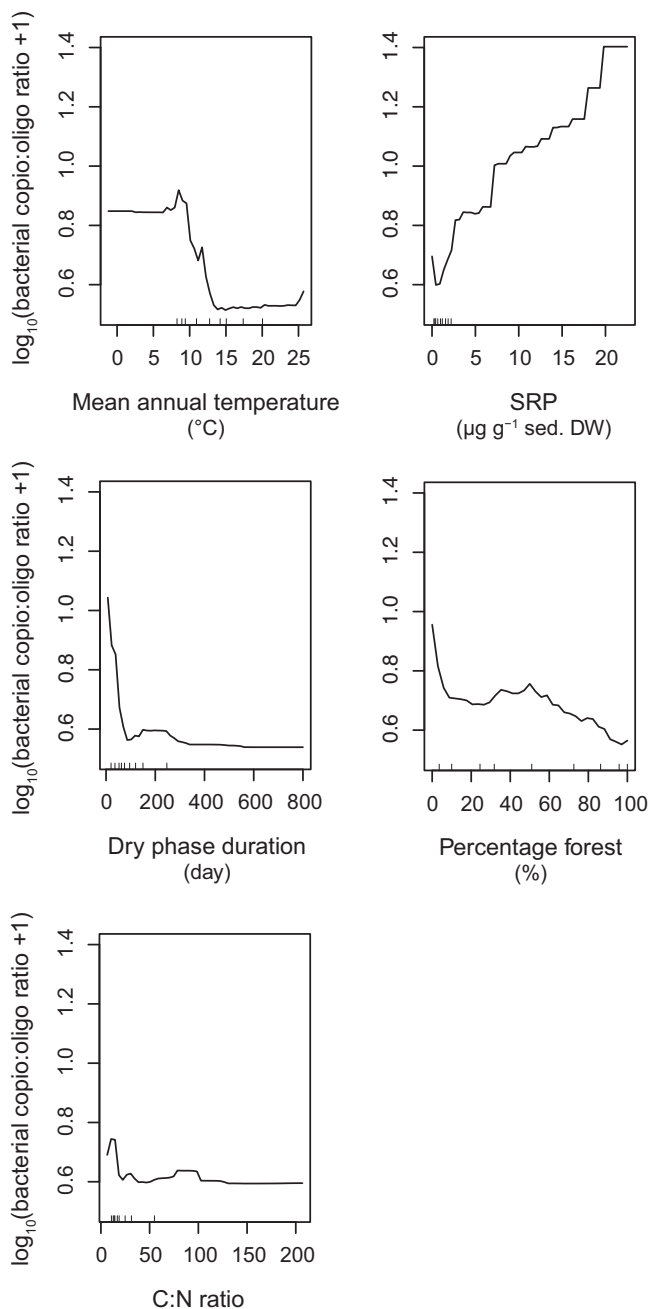


Fig. 4 | Influence of environmental variables on the bacterial copiotrophic:oligotrophic ratio. Partial dependence plots of the relative abundance of bacterial copiotrophic and oligotrophic operational taxonomic units (OTUs), indicating the contribution of five predictor variables to $\log_{10}(\text{copiotrophic:oligotrophic} [\text{copio:oligo}] \text{ ratio} + 1)$ as a function of the predictors (i.e. when the other contributing predictors are held at their mean). Hash marks on x axes indicate the deciles of the predictor variables. Predictors are shown in order of decreasing importance (%IncMse as defined in Table 1).

oligotrophic strategy. These oligotrophs likely outcompeted copiotrophs in dry conditions owing to their greater resistance to osmotic stress and higher investment in extracellular enzyme machinery, allowing them to cope with reduced substrate diffusion^{30,50,51}. The selection of oligotrophic taxa under dry conditions might explain reported increases in the relative abundance of Actinobacteria and Alphaproteobacteria and decreases in that of Betaproteobacteria and Bacteroidetes in response to sediment desiccation^{32,52}. These results suggest that mechanisms underlying the assembly of bacterial

communities exposed to drying operate through adaptations to reduced water and resource availability, potentially leading to a progressive shift toward terrestrial soil communities in NPRs during prolonged dry phases²⁸.

Such mechanisms could also apply to fungal communities, as sediment drying can promote an increase in the abundance of Basidiomycota³², which are oligotrophs and are more resistant to dry conditions than copiotrophic Ascomycota⁵⁰. Freshwater fungal communities are generally dominated by Ascomycota and Chytridiomycota, whereas Basidiomycota are much more common in terrestrial habitats^{20,53}. However, although Basidiomycota were particularly abundant in our dry-riverbed samples, we found no evidence that dry-phase durations affected the ratio of Ascomycota to Basidiomycota. Instead, the relative abundance of Basidiomycota increased with increasing sediment C:N and riparian cover, suggesting that inputs of complex organic matter in the form of plant litter promoted fungal taxa which can degrade recalcitrant polymers such as lignin⁵⁴. The selection of distinct ecological strategies under dry conditions could alter organic matter decomposition and nutrient cycling⁵¹.

Our results provide new insight into the biodiversity patterns of a broad range of taxa that have been largely overlooked in NPRs. For example, Ciliophora and Cercozoa dominated the protozoan community, as reported in soils⁵⁵, and the sediments of perennial rivers⁵⁶, temporary ponds, and other NPRs⁵⁷. Protozoa play a key role in structuring microbial food webs through their consumption of Bacteria, Fungi, Algae, and detrital matter⁵⁸. During dry phases, the relative contribution of Protozoa to carbon and nutrient cycling might increase due to their greater tolerance of harsh environmental conditions than larger taxa^{20,59}.

Most Metazoa identified by our metabarcoding approach were Arthropoda such as Collembola, Ostracoda, Arachnida (mainly mites), and Nematoda, representing some important meiofauna groups, whereas macroinvertebrate eDNA was poorly detected. Sediments can provide a refuge for some aquatic invertebrates during dry phases⁶⁰, promoting their detection by eDNA analyses. In contrast, our detected arthropod community was dominated by largely terrestrial taxa such as Collembola and Arachnida, supporting previous reports that colonization of dry riverbeds by terrestrial arthropods from adjacent riparian areas contributes to dry-phase community assembly^{36,49}. Other invertebrates, such as Nematoda and freshwater Ostracoda, can survive for long periods in dry riverbeds as dormant, desiccation-tolerant eggs⁶¹.

Rarefaction curves indicated that our sequencing depth was sufficient to capture the diversity of eukaryotic organisms in dry riverbeds (Fig. S26) but that part of the bacterial diversity in our samples remained undetected (Fig. S27). Although increasing the sequencing depth may have identified additional and potentially rare bacterial OTUs, the number of reads selected for rarefaction was sufficient to identify trends and relative variation in alpha-diversity among samples⁶² without altering our estimates of beta-diversity^{63,64}.

Tight linkages between beta-diversity across multiple taxa

Contrary to our second hypothesis, we did not identify strong relationships between environmental variables, spatial distances, and the beta-diversity of different taxa in dry riverbeds. Instead, most relationships were between the beta-diversity of different taxa, suggesting that biotic interactions had a stronger influence on community composition than environmental conditions or dispersal constraints. The strong correlation between the beta-diversity of Bacteria and Fungi could reflect biotic interactions such as competition for organic carbon and nutrients or facilitation. For example, Bacteria benefit from the labile molecules released by the enzymatic degradation of complex polymers by Fungi⁶⁵. Similarly, the observed association between the beta-diversity of Bacteria and Algae could reflect bacterial consumption of algal exudates⁶⁶. Strong associations between the beta-

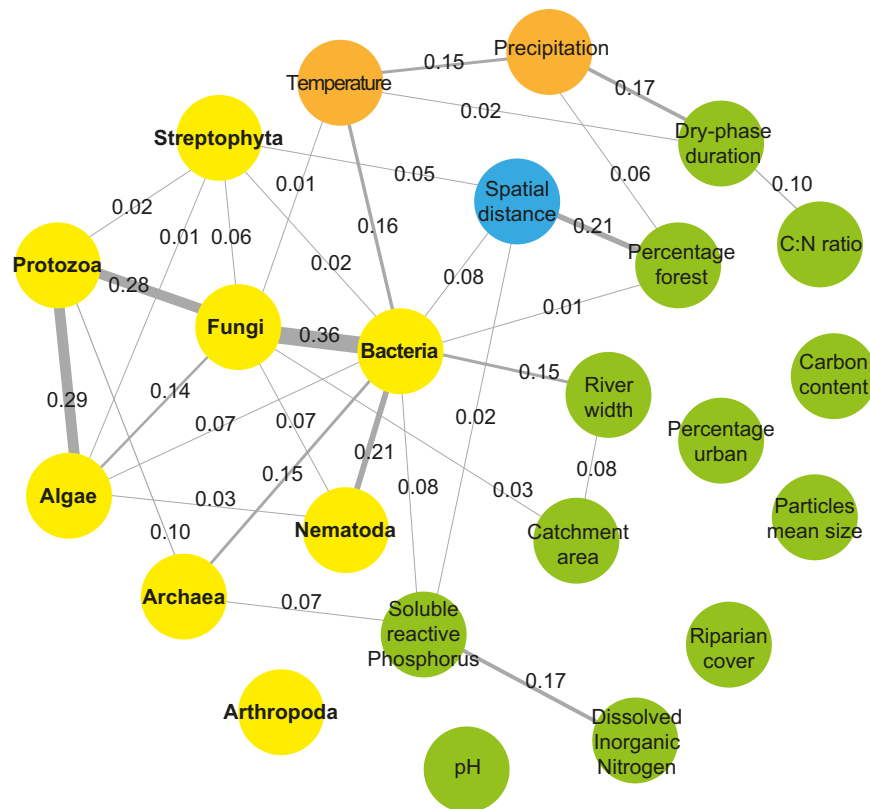


Fig. 5 | Partial correlation network between the beta-diversity of the eight major taxa contributing to dry-riverbed biodiversity and climatic, physico-chemical, land-use, and spatial distances between sites, as inferred from a graphical lasso method. Each node represents the turnover component of beta-

diversity (calculated using the Bray-Curtis index) of a taxon (yellow) or a spatial (blue), climatic (orange), or environmental (green) distance. Line width is proportional to the partial correlations (indicated on each line) between pairs of nodes.

diversity of Protozoa and both Fungi and Algae also occur in perennial rivers⁴⁴ and could reflect consumption of Algae and Fungi by protozoans⁶⁷. Similar relationships were observed between the beta-diversity of Nematoda and Bacteria, and to a lesser extent between Algae and Fungi, in line with the different feeding habits of Nematoda⁶⁸. Arthropoda were the only group whose beta-diversity did not closely correlate with that of other taxa, despite the potential of arthropods to control the structure of riverbed microbial decomposer and primary producer communities¹⁹.

The observed limited influence of dispersal on the composition of dry-riverbed communities should be interpreted with caution, because our sites spanned many river networks and our Euclidean measure of spatial distances did not account for hydrological connectivity among sites. Hydrological connectivity is likely to constrain the movement of aquatic taxa, which could thus have led to underestimation of the role of dispersal²². Given the low explanatory power of the variables included in the random forest models of OTU richness for some taxa, the weak correlations between environmental variables and the beta-diversity of most taxa also suggest a limited influence of environmental filtering on community assembly in dry riverbeds. This finding is surprising, because the analyzed environmental variables (e.g., organic carbon content, pH, temperature) are known drivers of soil and freshwater microbial diversity^{55,69,70}.

Biodiversity–environment relationships may have been partially obscured by dormant or dead aquatic organisms detected in dry sediments by eDNA metabarcoding. In addition, samples were collected at sites with different drying histories. At sites that have experienced seasonal dry phases over evolutionary timescales, some aquatic species have evolved specific adaptations to tolerate dry phases. In contrast, at newly intermittent sites communities may be prone to higher biodiversity loss in response to unprecedented drying

events⁶. Another non-exclusive explanation for the weak effect of environmental variables on beta-diversity could be that the observed strong partial relationships between taxa also reflect unmeasured environmental variables. This would imply the limited relevance of our measured variables, which is unlikely given the body of evidence of their biotic effects. Finally, the relationships inferred between changes in the community composition of different taxa may also reflect long-term co-evolution among these taxa. Such co-evolutionary processes involve biotic interactions and may also hide subtler biogeographic histories underlying community assembly.

Study limitations

Our results should be interpreted in light of limitations associated with our sampling design and eDNA metabarcoding approach. First, our large-scale assessment was biased towards temperate and, to a lesser extent, arid climates, which is a frequent limitation of global biodiversity studies^{71,72}. Future research is needed to improve the global coverage of NPR biodiversity, particularly in boreal, continental, polar and tropical climate zones. Second, potential biases are associated with metabarcoding analyses targeting eDNA from sediments, which comprises intracellular DNA in active, dormant and dead cells as well as actively or passively released extracellular DNA⁷³. Reliance on eDNA can thus inflate biodiversity estimates and obscure environment-biota relationships. However, even if relic DNA accounts for a significant proportion of the total DNA pool, estimates are likely only partially biased⁷⁴, because all eDNA reflects either present or past organisms and thus communities. Coupling eDNA with eRNA approaches can improve assessments of the contribution of active and inactive organisms to biodiversity estimates⁷⁵, despite the methodological constraints of eRNA approaches⁴¹. Third, methodological differences between morphology-based and molecular approaches, and among

molecular analysis protocols, complicate comparison of biodiversity patterns documented by different studies. Harmonizing the molecular approaches and workflows used to characterize communities during dry and wet phases could thus provide a more complete picture of the aquatic–terrestrial biodiversity of NPRs.

As temperatures and aridity increase in many global regions due to ongoing climate change, NPRs are becoming increasingly prevalent in both space and time. Our results suggest that the biodiversity of most major taxa in dry riverbeds is likely to be increasingly affected by increasing climatic extremity, especially under conditions of low resource availability. Management strategies are thus needed to support the biodiversity and thus ecosystem functions and services of NPRs affected by diminishing flows⁷⁶. In addition, the tight linkages we observed between the beta-diversity of multiple major taxa in dry riverbeds suggest that recognizing biotic interactions in such strategies could maximize the effectiveness of actions taken to protect biodiverse NPR communities as they adapt to longer, more frequent and higher-intensity dry phases.

Methods

Sample and data collection

This research complies with all relevant ethical regulations and the samples have been collected and exported with the necessary permissions. Sediment samples were collected by an international consortium⁷⁷ (<https://1000irp.hub.inrae.fr/>) following a standardized protocol during dry phases in the years 2015–2016. A total of 84 samples were included in our statistical analyses (see information below). These samples were collected in 19 countries spanning the main five Köppen climate classes (tropical $n=2$, dry $n=14$, temperate $n=66$, continental $n=1$, polar $n=1$) (Fig. 1). The length of each sampled river reach was defined as $10\times$ the average active channel width, to cover a representative area and to ensure consistent sampling effort. The active channel was defined as the area of inundated and exposed riverbed sediments between clearly delineated edges of perennial terrestrial vegetation and/or abrupt changes in bank slope. Within each reach, 5% of the riverbed was randomly sampled with 1-m² quadrats to collect a total of 3 L of sediments. Riverbed sediment samples were collected from each quadrat (sediment depth: 0–10 cm) and pooled into a single composite sample per site. This sample encompassed within-reach variability in dry riverbed habitats, including areas with different drying patterns, and their associated biodiversity. In the laboratory, sediments were sieved (2 mm) and air-dried for 1 week⁷⁸. To minimize the risk of cross-contamination, sieves were sterilized using 10% bleach between processing of samples from different sites. For physicochemical analyses, a homogenized -160-g subsample was packed in air-tight plastic containers and shipped to one of two laboratories for analysis^{15,17}. Upon receipt, samples were stored in a dry and dark room for later analyses. For eDNA metabarcoding, a homogenized subsample of -40 g was packed in air-tight plastic containers and sent to the Laboratoire d'Écologie Alpine (Université Grenoble Alpes, France), where the samples were immediately stored at -20 °C before further processing. These simple preservation and storage measures were designed to maximize the number of surveyed sites, including sites in remote areas and where effective chemicals for DNA preservation⁷⁹ are not readily available. Moreover, the potential effects of sample storage conditions on large-scale comparisons of soil communities are small⁸⁰.

The latitude and longitude (WGS84 datum) of each sampling site was determined in the field with a geographic positioning system or later in the laboratory using a geographic information system (GIS). Mean annual precipitation (mm) and mean annual temperature (°C) were estimated based on the WorldClim 1.4. database (<http://www.worldclim.org>), which provides 1-km spatial resolution climate surfaces for global land areas over the period 1970–2000. The dry-phase duration (i.e., the period between the onset of the dry phase and

sample collection) was estimated either based on logger data or fortnightly observations. River width and riparian canopy cover (visual estimates of the proportion of the river reach covered by vegetation) were estimated in the field. These local-scale variables (apart from land cover) were recorded in situ by consortium participants using a standardized protocol⁷⁷. The proportion of the catchment area upstream of the sampling site covered by forest, agricultural land or urban areas (%) was determined by each participant using local knowledge or GIS-based information derived from the most up-to-date national land cover maps for each country.

The organic carbon (C) and total nitrogen (N) content of sediment samples was determined using elemental analyzers; sediment texture (% sand, silt and clay; mean and median particle size) with a laser diffractometer; and dissolved organic carbon, SRP and DIN as the sum of extractable ammonium (NH₄⁺) and nitrate (NO₃⁻), using standard analytical methods¹⁵.

eDNA metabarcoding

Sediment biodiversity was estimated using markers amplifying both Bacteria and Archaea (16S rDNA, Bact02, forward primer: GCCAGCMGCCGCGGTAA, reverse primer: GGACTACCMGGGTATC TAA)³⁹ and all Eukaryota (18S nuclear rDNA, Euka02, forward primer: TTTGTCTGTTAATTSCG, reverse primer: CACAGACCTGTATTGC)⁸¹. We opted for 18S primers to meet our main aim of capturing a broad suite of eukaryotic taxa, including Algae, Protozoa, Metazoa, and Fungi⁴⁴. Although the internal transcribed spacer (ITS) is the preferred target for Fungi, 18S is also informative⁸², and both ITS and 18S markers have limitations and introduce biases, particularly in fungal community analyses⁸³. Extracellular DNA was extracted from 10 g of sediment by adding an equivalent volume of saturated phosphate buffer (Na₂HPO₄; 0.12 M; pH ≈ 8) before agitation for 15 min on an orbital shaker³⁹. A 2-mL volume of the resulting suspension was centrifuged at 10,000 *g* for 5 min, and a 400-μL aliquot of the supernatant was then used as the starting material for eDNA extraction using the NucleoSpin Soil extraction kit (Macherey-Nagel) following the manufacturer's instructions except for the cell lysis step. Blank extraction controls using only phosphate buffer were included in the extraction protocol. Polymerase chain reactions (PCR) were run in triplicate for each DNA extract and each marker, along with negative controls in which the DNA extract was replaced by molecular-grade water. The amplification mix consisted of 2× Applied BiosystemsTM MasterMix AmpliTaq GoldTM 360, 0.5 μM of each tagged forward and reverse primer, and 3.2 μg/mL of bovine serum albumin in a final reaction volume of 20 μL, including 2 μL of extracted DNA. PCR conditions for the amplification of the Bact02 marker comprised 48 cycles of 30 s at 95 °C, 30 s at 53 °C and 90 s at 72 °C. The 18S marker was amplified by 45 cycles of 30 s at 95 °C, 30 s at 45 °C, and 1 min at 72 °C. For each marker, PCR products were visualized by capillary electrophoresis on a QIAxcel (Qiagen). PCR products (including extraction and negative controls) were pooled for each marker and eight 200-μL aliquots were purified using the MinElute PCR purification kit (Qiagen). Purified products were then pooled before sequencing. Library preparation and sequencing were performed at FASTERIS (Geneva, Switzerland) using the Metafast PCR-free protocol (www.fasteris.com/en-us/NGS/DNA-sequencing/Metabarcoding/Metagenomics-16S-18S-ITS-or-custom-PCR-amplicons). High-throughput sequencing of the 18S marker was performed on an Illumina HiSeq 2500 platform (2 × 150 bp paired-end reads) and 16S amplicons were sequenced on an Illumina MiSeq (2 × 250 bp paired-end reads) platform.

The sequencing data were curated using the OBITools software package⁸⁴ together with custom R scripts. Paired-end reads were assembled based on overlapping 3'-end sequences, assigned to the respective sample/marker, and de-replicated. Singletons, sequences shorter than the expected amplicon size, and sequences present in only one PCR replicate were removed before using the *obiclean* command to remove PCR errors. We formed operational taxonomic units

(OTUs) by clustering sequences at 97% similarity using the SUMA-CLUST algorithm⁸⁵. OTU abundance was defined as the sum of reads sharing these similar sequences. In subsequent analyses, each OTU was represented by its most abundant sequence. Each OTU was assigned a taxonomic clade with the *ecotag* command⁸⁴, using a set of reference databases built with the *ecoPCR* software from the EMBL database version 136 to refine taxonomic annotations. Taxonomic annotations with >80% identities were retained. OTUs peaking in abundance in blank extractions or negative controls were considered contaminants and removed. PCR replicates with a number of reads and OTUs lower than or similar to negative controls were considered as dysfunctional PCRs and also removed³⁹. Finally, we removed PCR replicates that had a high Bray-Curtis dissimilarity compared to other PCR replicates from the same sample. PCR replicates were then pooled for each site. The number of reads, OTUs, samples, and PCR replicates at the different steps of the data curation procedure are reported in Table S2. A total of 152 sites were retained for the 18S marker and 167 sites for the 16S marker. Prior to statistical analysis, the 18S and 16S datasets were rarefied to 15624 and 2311 reads per site, resulting in a total of 76 and 84 sites, respectively. Most rarefaction curves for the 18S (Eukaryota) marker reached a plateau, indicating that the sequencing depth was adequate to detect the diversity of selected taxa in our samples (Fig. S26). Rarefaction curves approached the plateau for the 16S marker for Bacteria and Archaea but continued to increase with increasing sequencing depth (Fig. S27).

Based on previous classifications^{54,86}, we assigned major taxa within the Bacteria and Fungi to one of two distinct ecological strategies, copiotrophy or oligotrophy. Members of the classes Betaproteobacteria and Gammaproteobacteria and the phyla Bacteroidetes and Firmicutes were classified as copiotrophic, and members of the classes Alphaproteobacteria and Deltaproteobacteria and the phyla Acidobacteria, Actinobacteria and Chloroflexi were considered oligotrophic. Fungal taxa in the phylum Ascomycota were classified as copiotrophic, and Basidiomycota as oligotrophic.

Statistical analyses

All statistical analyses were conducted in R 3.6.2⁸⁷. We first identified the drivers of local biodiversity (alpha-diversity based on OTU richness) for eight major taxa, selected on the basis of OTU abundances and the functional significance of different taxa in freshwater ecosystems: Algae, Archaea, Bacteria, Fungi, Protozoa, Arthropoda, Nematoda and Streptophyta. We then analyzed the co-distribution and drivers of each of these eight taxa by linking their beta-diversity with that of other taxa (based on the Bray-Curtis dissimilarity index) and with environmental and spatial distances among samples.

For each sample and taxon, OTU richness was estimated using the abundance-based bias-corrected Chao1 estimate⁸⁸ with the “*estimateR*” function in the *vegan* package⁸⁹ to account for potentially undetected OTUs. The relative contribution of climatic (precipitation, temperature, dry-phase duration) and other environmental variables characterizing physicochemical conditions and land use (pH, organic carbon content, C:N ratio, DIN, SRP, mean sediment particle size, catchment area, channel width, riparian cover, % forest and urban land cover in the catchment) to the estimated OTU richness of the eight taxa was assessed using random forest models (i.e., one model for each taxon) using the *randomForest* package⁹⁰. Latitude can act a proxy for a wide range of environmental variables and was strongly ($|r| > 0.7$)⁹¹ correlated with mean annual temperature ($r = -0.82$, $p < 0.05$, Fig. S28), so was excluded from the analysis of OTU richness. The percentage of forest and agricultural land cover in the catchment were strongly negatively correlated ($r = -0.95$, $p < 0.05$, Fig. S28), so only the percentage of forest was included in the analyses. Random forest models are particularly well-suited to handle nonlinear relationships between response variables and predictors as well as complex interactions among predictors⁹². These models provide a measure (R^2)

indicating the model’s overall goodness of fit and a procedure to estimate the importance of each variable included. Importance measures provide the contribution of variables to model accuracy and are obtained from the degradation in model performance when a predictor is randomly permuted⁹³. The inclusion of irrelevant variables can decrease model performance⁹⁴. Consequently, we selected variables with the recursive feature elimination algorithm⁹⁵ by iteratively training the model for each taxon, inspecting the variable importance plot, and then removing the lowest ranked variable until reaching the best model, as indicated by the % variance explained. Partial dependence plots, which show the marginal contribution of a predictor variable to the response (i.e., the response as a function of the predictor when all other predictors are kept at their mean values), were used to interpret relationships between OTU richness ($\log_{10}[x + 1]$ -transformed prior to analyses) and predictors.

Using the same approach, we explored the drivers of changes in the ecological strategies (copiotrophy vs oligotrophy) of Bacteria and Fungi communities in dry riverbeds. The relative contributions of climatic, physicochemical and land-use variables on the copiotrophic:oligotrophic ratios (obtained by dividing the summed abundances of copiotrophic OTUs by the summed abundances of oligotrophic OTUs and $\log_{10}[x + 1]$ -transformed prior to analyses) were assessed using random forests models as described above.

For each of the eight taxa, a community dissimilarity matrix was computed based on Bray-Curtis distances between all pairs of samples, after applying the Hellinger transformation to the OTU abundance matrix to downweight the influence of zero values and rare species⁹⁶ using the “*decostand*” function from the *vegan* package⁸⁹. Beta-diversity patterns were visualized using principal coordinates analysis (PCoA) with the “*pcoa*” function from the *ape* package⁹⁷. Permutational multivariate analysis of variance (PERMANOVA) was then used to assess whether community composition differed between continents (Africa, America, Eurasia, and Oceania), climate classes, and their interaction, using the “*adonis2*” function in the *vegan* package⁸⁹. Where significant differences were detected, we ran pairwise post-hoc tests using the “*pairwise.adonis*” function in the *pairwiseAdonis* package⁹⁸.

We used a graphical lasso approach⁹⁹ as described in ref. 100 to assess linkages among the beta-diversity of each taxon and climatic, physicochemical, and land-use variables, and spatial distances (Euclidean distances among sampling sites based on geographical coordinates). This statistical method allowed inference of partial correlations (i.e., for each pair of variables after taking other variables into account) between all variables from the inverse of the variance-covariance matrix, using a regularization penalty to set all spurious correlations to zero. Partial networks were estimated for different values of lambda (a tuning parameter that controls the level of sparsity of the network) whose optimal value was selected using the extended Bayesian information criterion implemented in the “*EBICglasso*” function in the *qgraph* package¹⁰¹. The obtained partial correlation network consisted of nodes representing the variables (beta-diversity of taxa or climatic, physicochemical, land-use, and spatial distances) and edges representing partial correlations between two variables (i.e., nodes). Two variables are considered connected when they are conditionally dependent on each other (i.e., they are correlated after accounting for the effects of other variables). If two variables are unconnected, they are considered conditionally independent (i.e., they have a partial correlation coefficient of zero and cannot causally influence each other). Assuming adequate representation of the major environmental variables, connections among nodes in partial correlation networks of beta-diversity between pairs of taxa can identify potential biotic interactions among taxa¹⁰⁰. We assessed the strength of the linkages between the beta-diversity of a given taxon and other taxa by analyzing the degree (i.e., number of directly connected nodes) and

weighted degree (i.e., total sum of partial correlations between a given node and other directly connected nodes) of the corresponding node in the network. Higher degree and weighted degree values indicate greater influence of a taxon on the beta-diversity of other taxa. This analysis was conducted on the subset of samples common to the Eukaryota and Bacteria datasets, which were then rarefied to 15883 and 2423 reads, respectively, leading to a total of 40 samples.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The data for this study have been deposited in the European Nucleotide Archive (ENA) at EMBL-EBI under accession number [PRJEB66196](https://doi.org/10.1038/s41467-024-50873-1). Curated metabarcoding and environmental data can be accessed from a Dryad repository (<https://doi.org/10.5061/dryad.v6wwpzh2j>). Source data are provided with this paper.

Code availability

The scripts used to obtain the results are available from the Dryad repository (<https://doi.org/10.5061/dryad.v6wwpzh2j>).

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A.F, T.D, R.C, D.vS and K.T assumed responsibility for the overall project planning and coordination. All authors collected sediments in their countries and processed and analyzed this material. The centralized metabarcoding analyses were conducted by A.F, D.R, and C.M. The bioinformatic curation process was performed by A.F with contributions by F.B. Statistical analyses were performed by A.F with contributions by M.O and W.T. A.F led the writing of the manuscript with notable contributions by T.D, R.S and M.O.G. A.B, A.B.M, A.E, A.L, A.M, A.M.D.G, A.P, A.Savić, A.Steward, A.T, A.U, A.Z, B.d.F.T, B.F, B.G, B.L, C.Leigh, C.Little, C.C, C.F, C.M.L, D.B, D.C.A, D.H.Z, D.N, E.B, E.I.M, E.J.M.S, F.A, F.D, G.L.G, G.P, I.G.B, I.Pagán, I.Pardo, J.B, J.C, J.H, J.I.J, J.M, K.Boersma, K.Brintrup, K.R.S, L.G.G, M.Miliša, M.Morais, M.B, M.C.M, M.D, M.I.A, M.L.B, M.M.S.M, M.O, M.P, N.Bonada, N.Bond, N.C, N.J.W, N.M, O.S, P.N, P.P, P.R.L, P.S.K, R.A, R.B, R.D.C, R.F.J, R.G, R.J.R, R.V.V, S.A, S.C, S.D.L, S.G, S.G, S.L, S.U.P, T.C, V.D.V, W.T and Y.V commented on and contributed to revising draft versions.

Competing interests

The authors declare no competing interests.

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