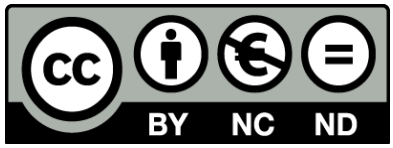


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Facing Global Change:

Impacts of drying and human pressures on invertebrate diversity and organic matter processing in a Mediterranean stream network

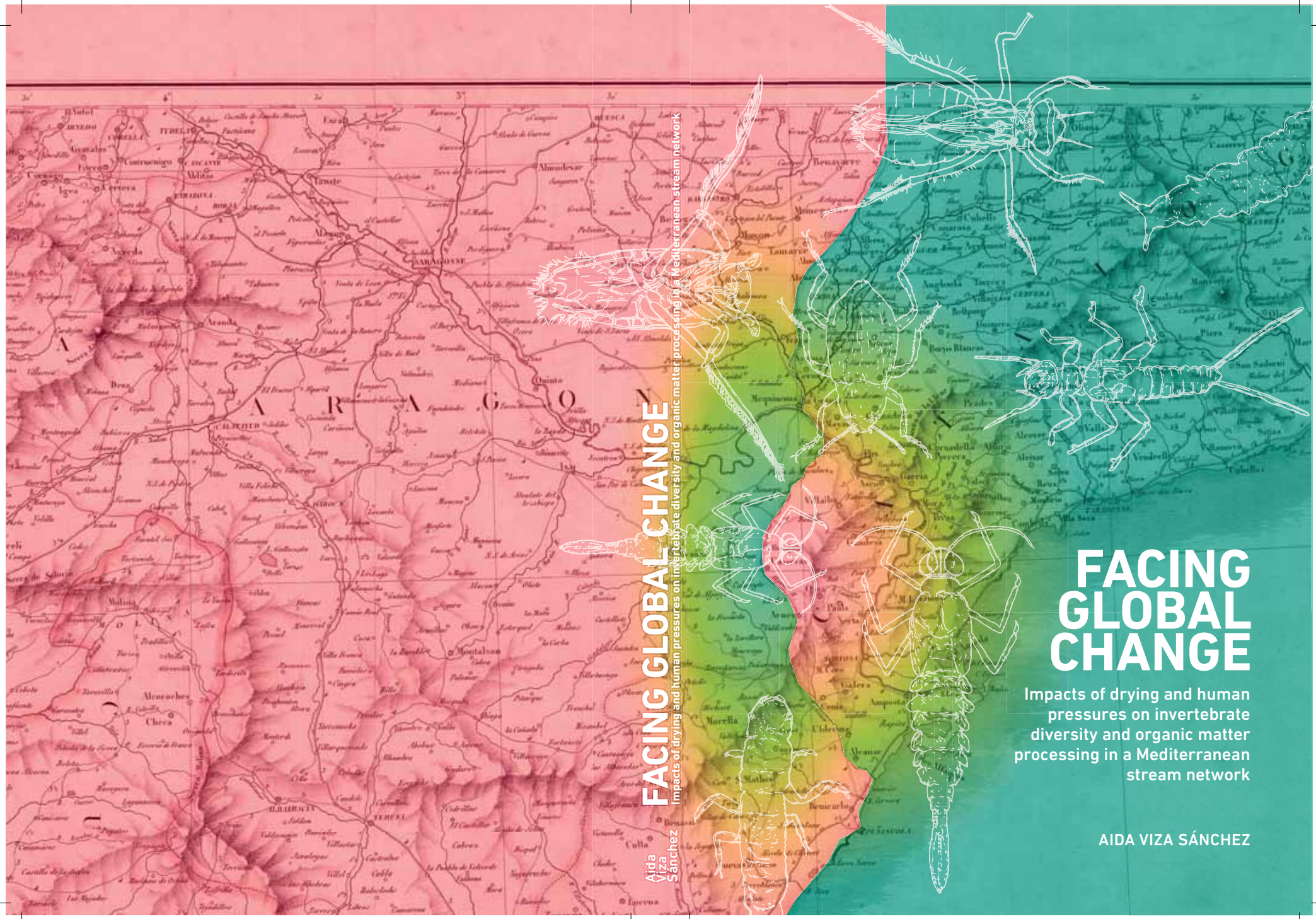
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FACING GLOBAL CHANGE

Impacts of drying and human pressures on invertebrate diversity and organic matter processing in a Mediterranean stream network

Aida Viza Sánchez

FACING GLOBAL CHANGE

Impacts of drying and human pressures on invertebrate diversity and organic matter processing in a Mediterranean stream network

AIDA VIZA SÁNCHEZ



UNIVERSITAT DE
BARCELONA

FACING GLOBAL CHANGE:
Impacts of drying and human pressures on invertebrate diversity and organic matter processing in a Mediterranean stream network

Aida Viza Sánchez

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Doctoral Thesis

Department of Evolutionary Biology, Ecology and Environmental Sciences
Doctoral program in Ecology, Environmental Sciences and Plant Physiology

Facing Global Change: Impacts of drying and human pressures on invertebrate diversity and organic matter processing in a Mediterranean stream network

Dissertation presented by Aida Viza Sánchez to apply for the doctoral degree by the Universitat de Barcelona

Aida Viza Sánchez
Barcelona, 2024



Approval of the directors of the doctoral thesis:

Dr. Isabel Muñoz Gracia
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Dr. Margarita Menéndez López
Associate profesor
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A les dones de casa,
que tot m'ho han donat

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ADVISORS' REPORT

Dr Isabel Muñoz and Dr Margarita Menéndez, professors in the Department of Evolutionary Biology, Ecology and Environmental Sciences (Ecology section), at the University of Barcelona, as supervisors of the Doctoral Thesis presented by Aida Viza Sánchez entitled: ***Facing global change: impacts of drying and human pressures on invertebrate diversity and organic matter processing in a Mediterranean stream network.***

INFORM,

That the research studies developed by Aida Viza Sánchez for her Doctoral Thesis have been organized in three chapters, which corresponds to three scientific papers, two already published, and the last in preparation to be sent in the next months.

This is the list of the published chapters, indicating the Journal Impact Factor according to SCI of ISI Web of Science:

- **Viza A.**, Arias-Real, R., Menéndez, M. and Muñoz, I. 2024. The role of seedbanks and hyporheic refuges in supporting benthic invertebrate community resistance and resilience to dry phases. **Aquatic Sciences**, 86 (1), 16. DOI: 10.1007/s00027-023-01034-x

The impact factor of the journal Aquatic Sciences in 2022 was 2.4. This journal is included in the category of Marine & Freshwater Biology with a SCIE 73.9, and it is reported in the Second Quartile being in the 29th position of the 109 journals included.

- **Viza A.**, Muñoz, I., Oliva F. and Menéndez, M. 2022. Contrary effects of flow intermittence and land uses on organic matter decomposition in a Mediterranean river. ***Science of the Total Environment***, 812, 151424. DOI: 10.1016/j.scitotenv.2021.151424.

The impact factor of Science of the Total Environment in 2022 was 9.8. This journal is included in the category of Environmental Sciences with a SCIE 90.7, and it is reported in the First Quartile being in the 20th position of the 334 journals included (1st Decile).

The manuscript in preparation is:

- Viza, A., Burgazzi, G., Menéndez, M., Schäfer B.R., and Muñoz, I. A comprehensive spatial analysis of invertebrate diversity within intermittent stream network: responses to drying and land uses.

And CERTIFY,

That Aida Viza Sánchez has participated actively on the development of the research and the elaboration associated to each of the papers listed. In particular, her contribution included the following tasks:

- Participation in setting objectives and in the experimental design of each one of the chapters developed
- Sampling design and field work
- Sample processing and analyses in laboratory
- Statistical data analyses and interpretation of results
- Writing, reviewing and editing processes of the manuscripts

Finally, we certify that the co-authors of the papers that conforms this Doctoral Thesis, will not use any of the manuscripts in another Doctoral Thesis.

Barcelona, 8th January 2024





Isabel Muñoz Gracia

Margarita Menéndez López

ABSTRACT

Intermittent rivers and ephemeral streams (IRES) currently constitute half of the global river network, occurring ubiquitously. Characterised by natural and periodic cessations of flow, IRES are proliferating due to global change, but face threats from different human-induced impacts such as water pollution, soil erosion, and habitat fragmentation. Notably, agriculture is one of the human activities with the greatest impact on freshwater ecosystems.

This thesis examines the effects of drying and different land uses (natural and agricultural) on biodiversity and ecosystem functioning in a Mediterranean intermittent stream network, the Algars. These aspects are crucial for sustaining biogeochemical cycles and energy transfer within a system. Additionally, the thesis investigates the role of resistance strategies during dry phases in preserving aquatic diversity. Chapter 1 focuses on the impact of drying and land use on the functional and taxonomic α- and β-diversity of aquatic invertebrate communities during a hydrological year. Chapter 2 evaluates the roles of hyporheic refuges and invertebrate seedbanks during the dry phase in benthic assemblages under flowing conditions, assessing the taxonomic and functional responses across six intermittent streams. Chapter 3 investigates the influence of drying and land use on organic matter (OM) decomposition and fungal biomass throughout an intermittent stream network during a hydrological year.

Chapter 1 reveals that drying negatively affects the taxonomic and functional α-diversity of aquatic invertebrates, but positively influences β-diversity. Land use predominantly affects α-diversity. Notably, habitat heterogeneity and elevated water nutrient levels in the stream network positively correlate with invertebrate diversity. The adverse effects of drying are less pronounced in upstream forested areas, which exhibit higher habitat heterogeneity, when compared to downstream agricultural regions. Chapter 2 identifies that seedbanks and hyporheic assemblages support up to 16% and 40% of the benthic assemblages, respectively. Diversity metrics vary between assemblage types in terms of taxonomic and functional richness. While no clear relationship can be established for diversity or the abundance of resistance traits with the dry phase duration, a negative linear relationship is observed between the abundance of resilience traits and the dry phase duration. Chapter 3 demonstrates that decomposition rates across the stream network negatively correlate with the duration of flow interruption. Dissolved inorganic nitrogen derived from agricultural activities mitigates the negative impact of drying on mass loss, enhancing it by up to threefold.

However, with prolonged dry conditions, this effect diminishes. Increased canopy cover, particularly in natural areas, enhances OM processing.

In summary, moderate agricultural activity within the small network studied can enhance diversity and ecosystem functioning. Nonetheless, increases in the frequency and duration of dry phases due to global change will reduce water availability, exacerbating the impacts of human pressures and threatening the survival strategies of aquatic species. This thesis significantly contributes to the understanding of the interactions between drying and land use in OM processing and biodiversity across a stream network. It underscores the importance of conserving natural and forested streams, especially in headwater regions, as potential refuges in intermittent networks.

CATALÀ

Els rius intermitents, rieres i torrents (IRES) actualment constitueixen la meitat de les conques fluvials mundials, existint arreu. Caracteritzats per interrupcions naturals i periòdiques del flux, els IRES s'expandeixen a causa del canvi global, però s'enfronten a altres amenaces derivades d'impactes humans com la contaminació de l'aigua, l'erosió del sòl i la fragmentació de l'hàbitat. L'agricultura és una de les activitats humanes amb major impacte en els ecosistemes d'aigua dolça.

Aquesta tesi examina els efectes de la sequera i els diferents usos del sòl (naturals i agrícoles) sobre la biodiversitat i el funcionament dels ecosistemes en una conca intermitent mediterrània, l'Algars. Aquests aspectes són crucials per mantenir els cicles biogeoquímics i la transferència d'energia dins del sistema. A més, l'estudi investiga el paper de les estratègies de resistència durant les fases seques en la preservació de la diversitat aquàtica.

El Capítol 1 es centra en l'impacte de la sequera i els usos del sòl en la α- i β-diversitat funcional i taxonòmica de les comunitats d'invertebrats aquàtics durant un any hidrològic. El Capítol 2 avalua els rols dels refugis hiporreics i dels bancs de llavors d'invertebrats durant la fase seca en les comunitats bentòniques sota condicions de flux, avaluant les respostes taxonòmiques i funcionals en quatre rieres i dos rius intermitents. El Capítol 3 investiga la influència de la sequera i els usos del sòl en la descomposició de la matèria orgànica (MO) i la biomassa de fongs al llarg de la conca de l'Algars durant un any hidrològic. Els resultats del Capítol 1 revelen que la sequera impacta negativament la α-diversitat funcional i taxonòmica dels invertebrats aquàtics, mentre que influeix positivament en la β-diversitat. Els diferents usos del sòl afecten predominantment la α-diversitat. A més a més, l'heterogeneïtat de l'hàbitat i els nivells elevats de nutrients de l'aigua dins de la conca correlacionen positivament amb la diversitat d'invertebrats. No obstant això, els efectes adversos de la sequera són

menys pronunciats en les zones boscoses riu amunt, que mostren una major heterogeneïtat de l'hàbitat, en comparació amb les regions agrícoles riu avall. El Capítol 2 identifica que les comunitats dels bancs de llavors i les hiporreiques representen fins a un 16% i un 40% de les comunitats bentònics, respectivament. Les mètriques de diversitat varien entre tipus de comunitat en termes de riquesa taxonòmica i funcional. Encara que no es pot establir una relació clara per la diversitat o l'abundància de trets de resistència amb la durada de la fase seca, s'observa una relació lineal negativa entre l'abundància de trets de resiliència i la durada de la fase seca. El Capítol 3 demostra que les taxes de descomposició a través de la conca d'estudi estan negativament relacionades amb la durada de la interrupció del flux. El nitrogen inorgànic dissolt associat amb l'agricultura mitiga l'impacte negatiu de la sequera sobre la pèrdua de massa, incrementant-la fins a tres vegades. Tot i així, aquest efecte disminueix amb fases seques més prolongades. Un major recobriment de la capçada, particularment en àrees naturals, millora el processament de la MO.

En resum, l'activitat agrícola moderada dins de la petita conca d'estudi pot millorar la diversitat i el funcionament de l'ecosistema. No obstant això, l'augment de la freqüència i la durada de les fases seques a causa del canvi global reduirà la disponibilitat d'aigua, exacerbant els impactes de les pressions humanes i amenaçant les estratègies de supervivència de la diversitat aquàtica. Aquesta tesi contribueix significativament a la comprensió de les interaccions entre la sequera i els usos del sòl en el processament de la MO i la biodiversitat a través d'una petita conca Mediterrània. A més, posa en rellevància la importància de conservar els rierols naturals i boscosos, especialment en les capçaleres, com a refugis potencials als IRES.

CASTELLANO

Los ríos intermitentes, arroyos y torrentes (IRES) actualmente constituyen la mitad de las cuencas fluviales mundiales, existiendo en todas partes. Caracterizados por interrupciones naturales y periódicas del flujo, los IRES se expanden debido al cambio global, pero enfrentan otras amenazas derivadas de impactos humanos como la contaminación del agua, la erosión del suelo y la fragmentación del hábitat. La agricultura es una de las actividades humanas con mayor impacto en los ecosistemas de agua dulce.

Esta tesis examina los efectos de la sequía y los diferentes usos del suelo (naturales y agrícolas) sobre la biodiversidad y el funcionamiento de los ecosistemas en una cuenca intermitente mediterránea, el Algars. Estos aspectos son cruciales para mantener los ciclos biogeoquímicos y la transferencia de energía dentro del sistema. Además, el estudio investiga el papel de las estrategias de resistencia durante las fases secas en la preservación de la diversidad acuática.

El Capítulo 1 se centra en el impacto de la sequía y los usos del suelo en la α- y β-diversidad funcional y taxonómica de las comunidades de invertebrados acuáticos durante un año hidrológico. El Capítulo 2 evalúa los roles de los refugios hiporreicos y de los bancos de semillas de invertebrados durante la fase seca en las comunidades bentónicas bajo condiciones de flujo, evaluando las respuestas taxonómicas y funcionales en cuatro arroyos y dos ríos intermitentes. El Capítulo 3 investiga la influencia de la sequía y los usos del suelo en la descomposición de la materia orgánica (MO) y la biomasa de hongos a lo largo de la cuenca del Algars durante un año hidrológico. Los resultados del Capítulo 1 revelan que la sequía impacta negativamente la α-diversidad funcional y taxonómica de los invertebrados acuáticos, mientras que influye positivamente en la β-diversidad. Los diferentes usos del suelo afectan predominantemente la α-diversidad. Además, la heterogeneidad del hábitat y los niveles elevados de nutrientes del agua dentro de la cuenca se correlacionan positivamente con la diversidad de invertebrados. Sin embargo, los efectos adversos de la sequía son menos pronunciados en las zonas boscosas río arriba, que muestran una mayor heterogeneidad del hábitat, en comparación con las regiones agrícolas río abajo. El Capítulo 2 identifica que las comunidades de los bancos de semillas y las hiporreicas representan hasta un 16% y un 40% de las comunidades bentónicas, respectivamente. Las métricas de diversidad varían entre tipos de comunidad en términos de riqueza taxonómica y funcional. Aunque no se puede establecer una relación clara para la diversidad o la abundancia de rasgos de resistencia con la duración de la fase seca, se observa una relación lineal negativa entre la abundancia de rasgos de resiliencia y la duración de la fase seca. El Capítulo 3 demuestra que las tasas de descomposición a través de la cuenca de estudio están negativamente relacionadas con la duración de la interrupción del flujo. El nitrógeno inorgánico disuelto asociado con la agricultura mitiga el impacto negativo de la sequía sobre la pérdida de masa, incrementándola hasta tres veces. Sin embargo, este efecto disminuye con fases secas más prolongadas. Un mayor recubrimiento del dosel, particularmente en áreas naturales, mejora el procesamiento de la MO.

En resumen, la actividad agrícola moderada dentro de la pequeña cuenca de estudio puede mejorar la diversidad y el funcionamiento del ecosistema. Sin embargo, el aumento en la frecuencia y la duración de las fases secas debido al cambio global reducirá la disponibilidad de agua, exacerbando los impactos de las presiones humanas y amenazando las estrategias de supervivencia de la diversidad acuática. Esta tesis contribuye significativamente a la comprensión de las interacciones entre la sequía y los usos del suelo en el procesamiento de MO y la biodiversidad a través de una pequeña cuenca Mediterránea. Además, resalta la importancia de conservar los

arroyos naturales y boscosos, especialmente en las cabeceras, como refugios potenciales en los IRES.

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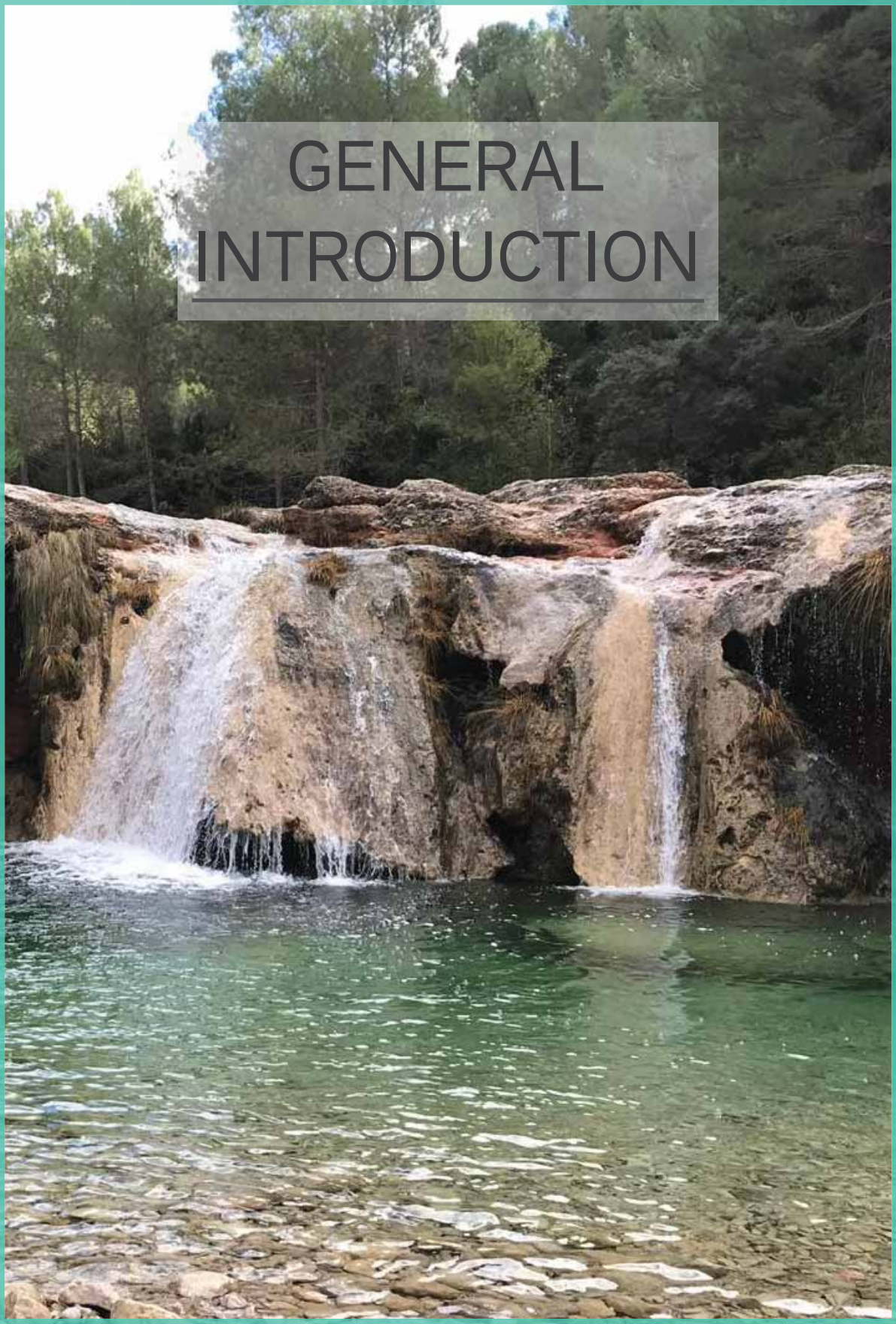
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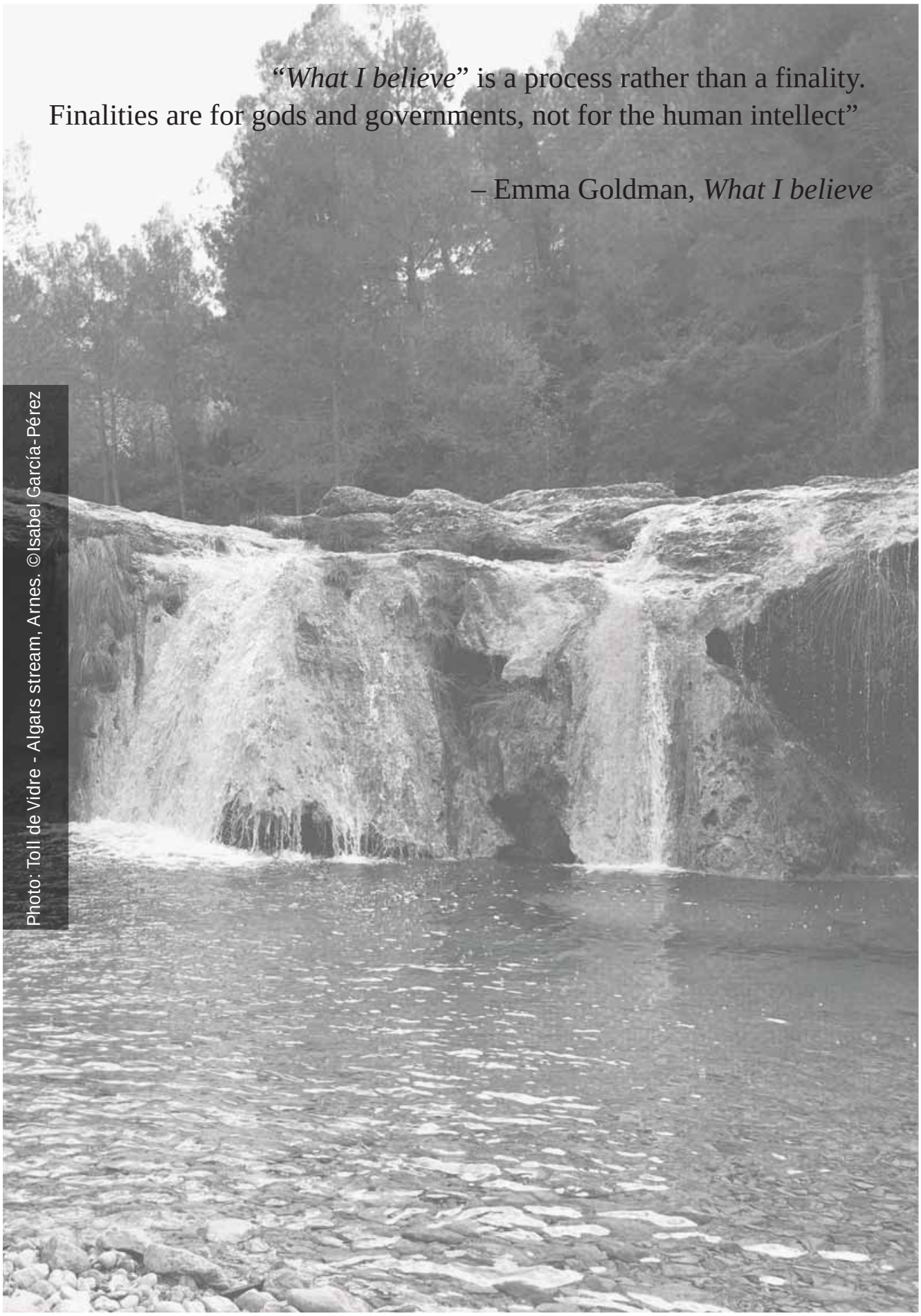
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GENERAL INTRODUCTION





"*What I believe*" is a process rather than a finality.
Finalities are for gods and governments, not for the human intellect"

– Emma Goldman, *What I believe*

Photo: Toll de Vidre - Algars stream, Arnes. ©Isabel García-Pérez

General Introduction

Freshwater systems are among the most threatened ecosystems worldwide, facing significant biodiversity loss due to human-induced climate change and anthropogenic activities such as flow alterations, pollution, habitat degradation and loss, and the introduction of non-native species (Jiménez Cisneros et al., 2014). Despite their vulnerability, freshwater ecosystems play a key role in supporting the wellbeing of humans by providing water resources, recreational opportunities, biodiversity, fisheries, and essential ecosystem functions (Aylward et al., 2005). However, in recent decades, the socio-economic development of human communities has led to unsustainable exploitation of freshwater resources and changes in land use, further contributing to the decline of natural ecosystems and biodiversity (Parmesan et al., 2022).

Rivers and streams, forming intricate fractal networks, drain continents, connect terrestrial and marine ecosystems, and transfer water, energy, and matter (Battin et al., 2023). These dynamic systems receive, transport, and process the equivalent of a terrestrial net ecosystem production (i.e., the difference between gross primary production and the community respiration of a given ecosystem) in their catchments (Aufdenkampe et al., 2011). Additionally, most rivers and streams worldwide experience natural drying, which interacts with human stressors in particularly complex and poorly understood ways, especially at the river network scale.

Intermittent Rivers and Ephemeral Streams (IRES)

Intermittent rivers and ephemeral streams (IRES) are characterised by periods of flow cessation in one or more sections along their networks. They are distributed worldwide, comprising over 50% of global watercourses (Messager et al., 2021). Flow intermittence (or drying) in IRES can occur naturally due to a combination of factors including climate, water source, and channel characteristics such as lithology and width (Datry et al., 2017). For instance, in arid and semiarid regions, flow disruption is driven by scarce precipitation and high temperatures, leading to increased evaporation and evapotranspiration. By contrast, in Alpine and Artic regions, flow cessation results

from water freezing in surface and shallow subsurface zones (Boulton & Lake, 1988; Davies et al., 1994; Paillex et al., 2020; Stanish et al., 2012). Natural IRES systems exhibit high biodiversity, containing species that are adapted to flow dynamics (including contraction, cessation, and resumption) and employ various strategies to cope with drying (Bogan et al., 2017). The process of flow interruption affects water chemistry and physical conditions, altering aquatic diversity, trait composition, and functions in IRES.

Human activities, such as water extraction, flow regulation, land-use, and climate change, can induce or modify flow intermittence in IRES (Steward et al., 2012). In recent decades, water demand has increased due to population and economic growth, resulting in intensified water extraction (Boretti & Rosa, 2019). Additionally, regions like the Mediterranean basin are expected to experience decreased rainfall and rising temperatures (Ali et al., 2023; Cramer et al., 2018). This, coupled with the growing human water demand, will lead to increased flow intermittence and alters in the dynamics of IRES networks (Chiu et al., 2017). Such changes will have impacts on biodiversity and ecosystem functioning in the network, subsequently affecting ecosystem services.

Flow regime

The flow regime of a river is defined as the temporal variability of streamflow at a specific section in the network (Nilsson & Renöfält, 2008; Poff et al., 1997). It encompasses five main components: magnitude, frequency, duration, timing, and rate of change of hydrological conditions (Figure I.1). In IRES, frequency and duration are the most common indices for characterising flow intermittence due to their ecological implications for biota and ecosystem processes (Larned et al., 2010). Dry phases in IRES exhibit wide variations that are influenced by regional and local factors such as climate, lithology, and vegetation in the catchment. These periods are the defining characteristic of the IRES flow regime. For instance, some river systems experience a unique seasonal period of flow intermittence (Boulton et al., 2014). By contrast, the upper parts of most headwater and low-order streams experience multiple, shorter periods of intermittent flow driven by rainfall (Datry et al., 2017). The variability in drying patterns directly affects all the dimensions of hydrological connectivity in the

IRES network, leading to complex intra- and interannual variability (Costigan et al., 2017). For instance, Mediterranean IRES are driven by sequential, predictable, seasonal events of flooding and drying, which determine the temporal and spatial dynamics of these systems (Gasith & Resh, 1999). In addition, while IRES segments in temperate regions are predominantly found in the headwaters (Kampf et al., 2021; Richardson & Danehy, 2007), they can occur throughout the entire network in arid and semiarid regions.

Hydrological connectivity

Drying periods disrupt hydrological connectivity, affecting physical, chemical, and biological processes. Hydrological connectivity in watercourses has three dimensions: longitudinal, lateral and vertical, which interact with the fourth dimension, time (Ward,

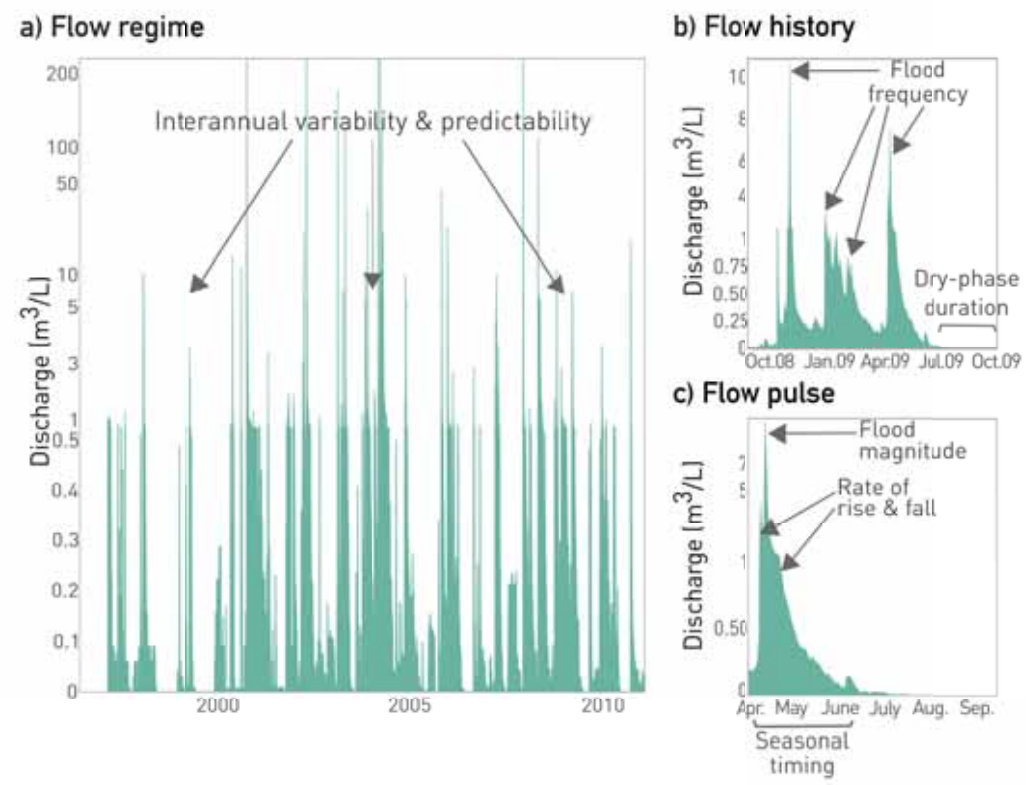


Figure I.1. Flow regime components of the Algars stream (measured at the gauging station in Batea, Spain) across three distinct temporal scales: a) multi-year data to illustrate interannual variability and predictability across all five components (see text); b) data from a single year, highlighting the dry phase duration and the seasonal timing of floods; and c) a single flow pulse, showing flood magnitude and rate changes. Adapted from Costigan et al., 2017.

1989). Longitudinal hydrological connectivity refers to the unidirectional flow of water from the headwaters to the river mouth that is driven by gravity (Boulton et al., 2017). It has implications for trends in geomorphology (e.g., channel width), hydrology (e.g., discharge), water chemistry (e.g., total dissolved solids), and ecology (e.g., aquatic biota distribution) (Allan & Castillo, 2007; Covino, 2017). Lateral hydrological connectivity links the main channel with the riparian area, including the aquatic habitats along the riparian zone and on the floodplain. Finally, vertical hydrological connectivity involves the exchange of water between the surface channel and the hyporheic zone, which comprises the shallow saturated sediments below. Connections and exchanges along the lateral and vertical dimensions can be bidirectional, governed by hydrological connectivity and local factors (Covino, 2017).

In IRES, the dynamic processes of expansion, contraction, and fragmentation across the spatial dimensions create a hydrological 'discontinuum' (Poole, 2002), interrupting one or more of the spatial dimensions. At the river network scale, these dynamics result in a mosaic of terrestrial and aquatic habitats constantly shift as a consequence of flow contraction and resumption (Datry, Larned, & Tockner, 2014). Although IRES exhibit different patterns of drying and rewetting based on regional and local factors, drying typically represents a gradual 'ramp' disturbance, while rewetting normally occurs faster (Figure I.2). In an intermittent reach, flow contraction occurs gradually, leading to the formation of remnant pools and interrupting the longitudinal and lateral connections. This precedes the total desiccation of the streambed that is also considered the desiccation (or dry) phase. During dry phases, vertical hydrological connectivity can also be interrupted, potentially leading to the complete dry up of the hyporheic zone. The dry phase ends with reduced evapotranspiration and the occurrence of rainfall or inputs of meltwater, after which flow resumes (expansion phase) (Larned et al., 2010).

The spatiotemporal location of drying in IRES network depends not only on local factors, but also on antecedent climate conditions, with precipitation in previous seasons and years having a particularly influential effect (Moidu et al., 2021). In different regions, increases in drought events and temperatures as result of human-

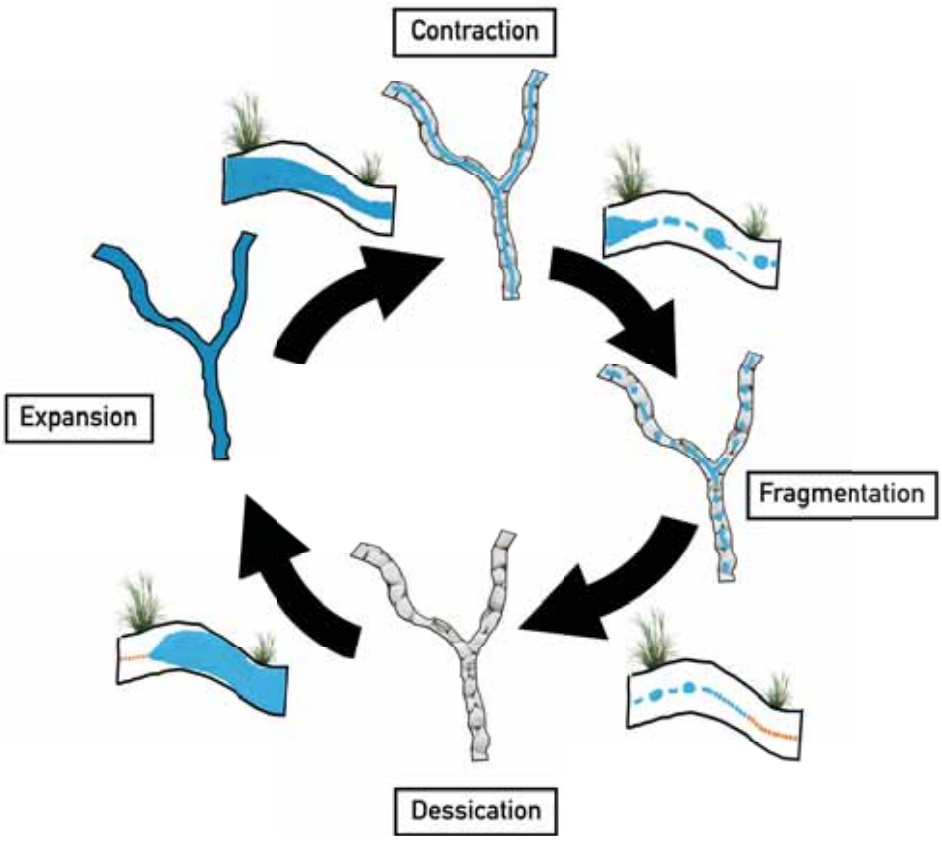


Figure I.2. Primary hydrological phases responsible for the temporal and spatial variations that are characteristic of IRES. The hydrological phases are represented with network illustrations and the transitions between the phases are depicted with illustrations of a stream reach profile. Adapted from Von Schiller et al., 2017.

induced climate change raise the probability and intensity of dry periods (seasonal or multi-year droughts) (Allen et al., 2020). This spatiotemporal extension of IRES may put biodiversity and ecosystem functioning at risk.

IRES biodiversity

In IRES, the dynamics of flow contraction and expansion drive species composition, abundance, and distribution throughout the network. During contraction phases, the network transforms into a continuously shifting mosaic of lotic (flowing), lentic (standing), and terrestrial habitats (Larned et al., 2010). This dynamism presents substantial challenges to both aquatic and terrestrial biota inhabiting the IRES. Nonetheless, IRES can support diverse biological communities, including various species of algae, macrophytes, invertebrates, amphibians, fish, reptiles, mammals,

and birds (Kerezsy et al., 2017; Sabater et al., 2017; Sánchez-Montoya et al., 2017; Steward et al., 2017; Stubbington, Bogan, et al., 2017).

Aquatic invertebrates from IRES are well-studied organisms and are classified by size as either macroinvertebrates (visible without magnification) or meiofauna (Stubbington, Bogan, et al., 2017). These invertebrates play important roles as shredders in detrital food-webs (see the 'OM decomposition in IRES' section), as herbivores in green food chains, and as prey for aquatic predators such as fish (Kerezsy et al., 2017). Additionally, they become prey to terrestrial predators, particularly when stranded in isolated pools or dry streambeds, and during the emergence of adult insects. This results in the transport of aquatic material to terrestrial habitats (Stubbington, Bogan, et al., 2017).

Spatiotemporal changes in IRES: effects on taxonomic diversity

The dynamic flow in IRES alters patterns of α- and β-diversity (BOX I.1). Specifically, as the dry-phase duration increases, the number of taxa decreases, resulting in a subset of species from nearby reaches that have shorter or no dry periods (Datry et al., 2014). This pattern reflects a nested community structure (BOX I.1). However, during flowing phases, the diversity in intermittent streams can rival or even exceed that of perennial streams, as observed in the Mediterranean region (Dolédec et al., 2017). IRES that are characterised by progressive drying exhibit fluctuating biodiversity along a temporal gradient (Stubbington, England, et al., 2017).

At the reach scale, under flowing conditions, the diversity in intermittent reaches is similar to that in perennial ones, influenced by similar biotic and abiotic factors due to full hydrological connectivity (Larned et al., 2010). As flow contraction phases begin, lateral hydrological connectivity is lost, leading to the disappearance of the taxa associated with streambank vegetation, such as the Hydroptilidae caddisflies, which feed on green plant cells (Marshall, 1978). As flow contraction progresses, flow velocities decrease, leading to a reduction in the number of lotic habitats and rheophilic taxa, like Nemouridae stoneflies that have high rheophilic affinity (Tachet et al., 2010). When flow ceases, intermittent sections begin to dry, fragmenting the river continuum. This process eliminates most rheophilic taxa, such as many species of mayflies, stoneflies, and caddisflies, that are collectively known as EPT (Ephemeroptera, Pleco-

BOX I.1 EXPLORING BIODIVERSITY AT MULTIPLE SCALES

The concept of diversity in a landscape is multifaceted and can be observed at three distinct scales: α-, β-, and γ-diversity (Figure B.2). While this Box primarily uses taxonomic diversity as an illustrative example, these concepts are equally pertinent to functional diversity (see Box I.2).

α-Diversity: This represents the local diversity within a specific assemblage or ecological unit, such as a pond or a stream reach. It focuses on the variety of taxa present in a single defined area.

β-Diversity: This scale highlights the differences in taxonomic composition between distinct assemblages. Historically conceptualised as the ratio between γ- and α-diversities, β-diversity is now commonly quantified using the Sorensen dissimilarity index. This index comprises two key components:

- **Richness difference**: This aspect captures the variation in taxonomic richness between assemblages. Such differences may stem from taxonomic reductions, leading to nestedness (Figure B.1a), a phenomenon where fewer species-rich subsets are included within richer sites. Alternatively, these differences can result from various ecological processes such as isolation due to the presence of physical barriers.
- **Species replacement**: This reflects the changes in taxonomic composition between assemblages. Often referred to as turnover (Figure B.1b), species replacement typically occurs when taxa replace one another along spatial or environmental gradients, such as in response to flow intermittence.

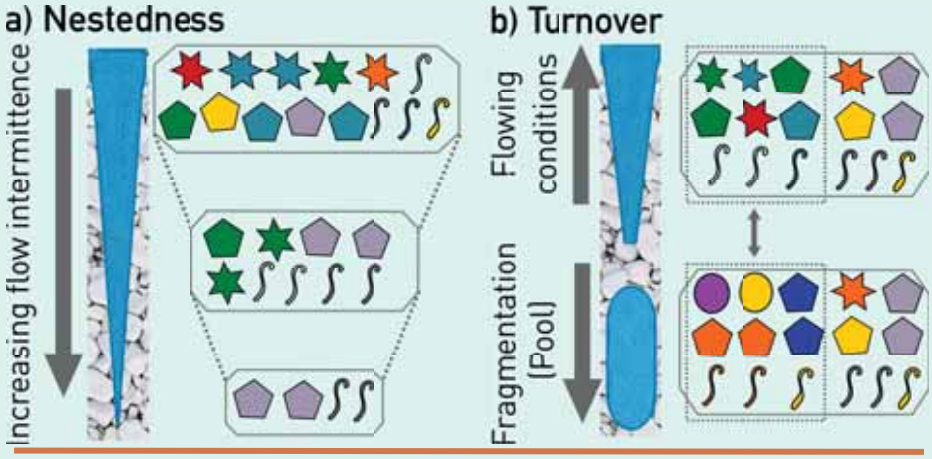


Figure B.1. **a) Nestedness:** Invertebrate taxon richness typically declines with increasing flow intermittence, with communities in the more intermittent reaches being nested subsets of those present at sites with greater flow permanence. **b) Turnover**: Invertebrate communities exhibit taxon replacement as in-stream conditions transition between flowing and pool phases. Different shapes represent different taxon groups, while colours represent varying trait compositions. Adapted from Stubbington et al., 2017.

BOX I.1 EXPLORING BIODIVERSITY AT MULTIPLE SCALES (continuation)

γ-Diversity: This scale represents the cumulative diversity across all habitats in a landscape. It is determined by the interplay of the α- and β-diversity components, providing a holistic view of landscape-level biodiversity.

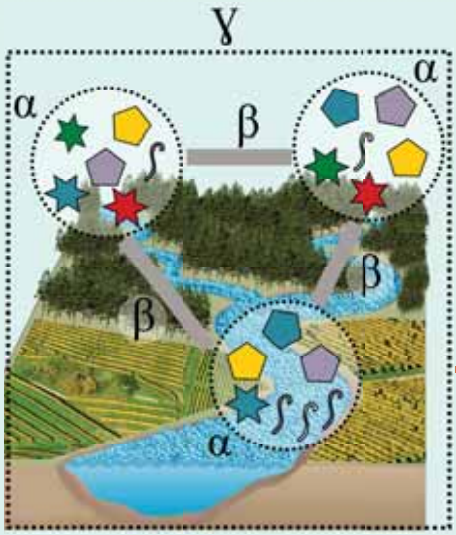


Figure B.2. Concept of diversity in a landscape. Different shapes represent different taxon groups, while colours represent varying trait compositions.

ptera, and Trichoptera) (Banegas-Medina et al., 2021). Lentic specialist species, such as true bugs and diving beetles, often replace the generalist taxa, particularly in remnant pools. These pools typically exhibit high water temperatures, high nutrient concentrations, and declining oxygen levels, leading to species replacement that is also known as turnover (Leigh et al., 2019; von Schiller et al., 2017; BOX I.1). In these environments, biotic interactions, particularly predation and resource competition, intensify (Datry et al., 2016).

During dry phases, terrestrial invertebrates colonise dry streambeds. Terrestrial and semiaquatic invertebrates can inhabit streambanks during wet phases and occupy the streambed during dry phases (Steward et al., 2017). Additionally, aquatic invertebrates in a desiccation-tolerant life stage can be found in dry streambeds, forming part of an 'invertebrate seedbank' (Stubbington & Datry, 2013). Upon flow resumption, aquatic conditions are restored, allowing aquatic biota to recolonize the reach. Aquatic invertebrates show varied recovery patterns, but, generally, recovery occurs within months (Bogan et al., 2017). These patterns depend on the dry-phase duration, local conditions, and the spatial configuration of aquatic refuges in the river

network (Stubbington, Bogan, et al., 2017). For instance, taxa using the hyporheic zone as a refuge during drying or arriving quickly by drift from upstream refuges can promptly return to the surface when flow resumes (Vander Vorste et al., 2016). During a complete hydrological cycle, IRES may show higher diversity levels than perennial reaches due to flow and habitat variability and the associated changes in species composition (Dolédec et al., 2017).

In IRES networks, diversity patterns may vary with the spatial location of the intermittent and perennial sections. For instance, in intermittent rivers with perennial headwaters, the number of taxa may decrease in the downstream direction, reflecting a greater distance from upstream refuges (Stubbington, Bogan, et al., 2017). Conversely, in IRES with patchy drying, species richness can remain stable along the network because local extinction rates are balanced by recolonisation from various perennial refuges in multiple directions that is facilitated by dispersal strategies, such as swimming, flying, and drift (Larned et al., 2010).

Spatiotemporal changes in IRES: effects on functional diversity

The functional diversity of invertebrate communities in IRES may differ from that in perennial watercourses due to the higher flow variability that leads to changes in habitat and food resource availability (Stubbington, Bogan, et al., 2017). A decrease in functional diversity is expected with increasing drying duration if the lost taxa possess unique traits not found in the remaining taxa. However, a certain level of functional redundancy (BOX I.2) may moderate this effect, suggesting that differences in functional diversity between perennial watercourses and IRES may be less pronounced than the differences in taxonomic diversity (Chanut et al., 2023). In harsh environmental systems, functional redundancy plays an important role, as functional diversity can remain stable despite decreasing taxonomic richness, reflecting the prevalence of taxa that show resistance or resilience to perturbations (Boersma et al., 2014).

Traits associated with survival during dry phases (see below), such as dormant life stages, may be more common in IRES during the dry season (Leigh et al., 2016). Feeding groups can also provide informative insights as changes in flow affect food resource availability. For instance, the filter feeders and shredders associated with the flowing phases disappear when flow ceases (Arias-Real et al., 2021). After the initial

BOX I.2 TAXONOMIC AND FUNCTIONAL DIVERSITY

TAXONOMIC DIVERSITY (TD)

TD encompasses the number and relative abundance of different taxa within an assemblage. Common measures of TD include:

- **Taxonomic richness (S):** The number of distinct taxa present in an assemblage, providing a fundamental biodiversity measure.
- **Shannon diversity index (H'):** Also known as the Shannon-Wiener index, this quantifies taxonomic diversity by considering both the number of taxa (richness) and their proportional abundance (evenness). The index reflects the uncertainty in predicting the identity of a randomly selected organism, linking species diversity to the concept of entropy (Shannon, 1948).

FUNCTIONAL DIVERSITY (FD)

FD refers to the number, type, and distribution of functions performed by the organisms in an assemblage (Díaz & Cabido, 2001). It primarily reflects the range of biological traits of the organisms within an assemblage or the functional trait space (FS) occupied. FS may be multidimensional, with each trait representing a separate dimension. Key metrics in the FS approach include:

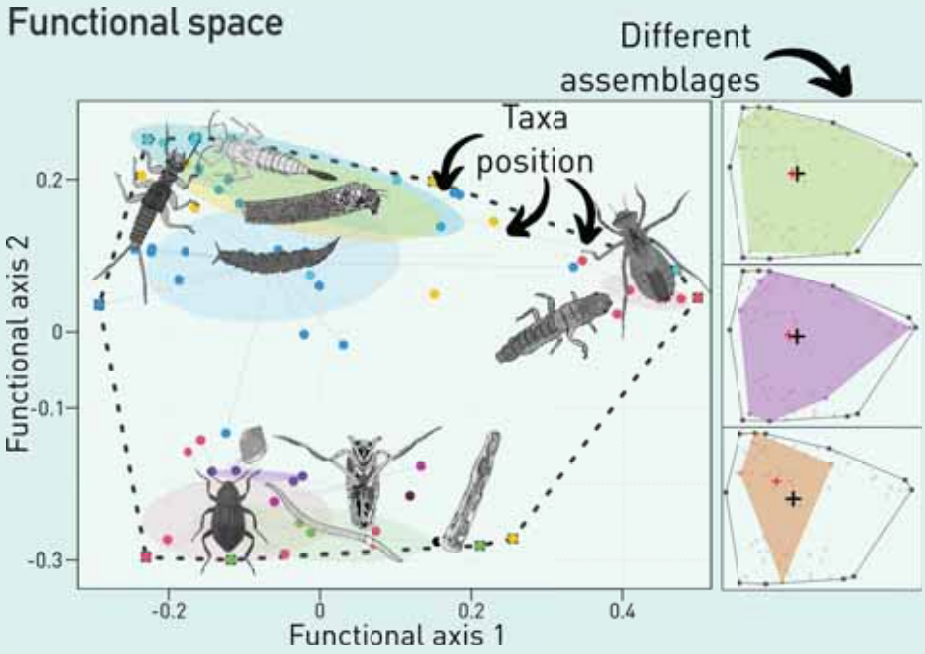


Figure B.3. Functional space represented through the trait composition of invertebrate communities. Taxa are positioned according to their respective trait compositions. Each assemblage occupies a distinct portion of space within this functional realm.

BOX I.2 TAXONOMIC AND FUNCTIONAL DIVERSITY (continuation)

- **Functional richness (FRic):** This captures the diversity of functions performed by different taxa within an assemblage. FRic is the minimum hypervolume of FS occupied by a set of taxa (Villéger et al., 2008). This index is related to taxonomic richness, without being weighted by taxon abundance.
- **Functional dispersion (FDis):** Focusing on the variation in trait abundances among the taxa (Kuebbing et al., 2018), FDis represents the weighted mean distance of each taxon to the centroid of their assemblage within the FS (Laliberté & Legendre, 2010).
- **Functional redundancy (FRed):** Addressing the ecological phenomenon where multiple taxa share similar ecological roles (Hubbell, 2005), FRed is crucial for the temporal stability of ecosystem functions. It buffers against the loss of specific species (Fischer & de Bello, 2023; Naeem, 1998). In FS terms, FRed is indicated by the overlap in the space occupied by different taxa or assemblages (Rosenfeld, 2002).

pulses of flow resumption, the number of taxa that feed on accumulated biofilm, acting as scrapers-grazers, increases (Álvarez & Pardo, 2009). Additionally, during the initial stages of flow resumption, pioneer taxa can complete their life-cycle with minimal competition from the later colonisers (Boulton & Lake, 1992).

Strategies for persisting in IRES

Freshwater species in IRES exhibit a wide range of strategies and traits to cope with drying. These traits and strategies may promote either resistance or resilience (Figure I.3) to survive perturbations. These perturbations consist of two parts: the disturbance (here, drying) and the biotic response to it (Lake, 2003). Resistance refers to the ability of an ecological unit, such as a population, to face a perturbation *in situ*, while resilience denotes the capacity of an organism or population to recolonise after the perturbation (Nimmo et al., 2015). For instance, some aquatic insects in IRES possess desiccation-tolerant life stages, such as dormant eggs or juveniles, enabling them to persist in dry streambeds as part of an 'invertebrate seedbank'. Other taxa recolonise intermittent reaches upon flow resumption by drifting from permanent reaches. While aquatic taxa in IRES display different resistance or resilience strategies to confront

drying, the terrestrial inhabitants of IRES must confront the opposite situation, dealing with periodic inundations of their terrestrial habitats (Steward et al., 2017).

Aquatic taxa in IRES employ several resistance mechanisms to withstand different levels of drying (Strachan et al., 2015). For example, aquatic insects with aerial respiration can survive in remnant pools, but cannot persist in completely dry streambeds without a desiccation-tolerant life stage. During flow cessation, aquatic taxa must have to tolerate the harsh conditions in the remaining aquatic habitats or have the capacity to enter a desiccation-resistant stage. The three most common resistance strategies of aquatic invertebrates in IRES are surviving in remnant pools, migrating to a hyporheic zone, and becoming part of an 'invertebrate seedbank' (Bogan et al., 2017; Figure I.3).

Flow cessation in IRES leads to habitat disconnection, resulting in aquatic invertebrates concentrating in remnant pools. In some IRES, insect abundance and richness in these refuges can be comparable to those in the flowing phases (Bonada et al., 2006). However, remnant pools can present harsh environments for aquatic organisms due to the loss of hydrological connectivity (see above). Many taxa either

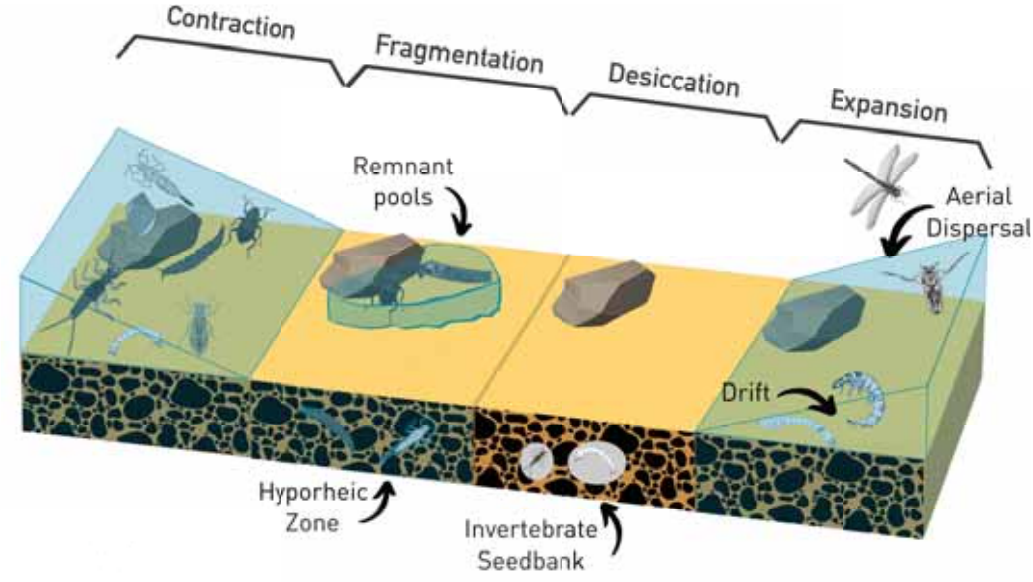


Figure I.3. Invertebrate strategies to cope with drying during different hydrological phases. During flow fragmentation, aquatic invertebrates can survive in situ (resistance) in remnant pools and hyporheic zones. During desiccation, survival is limited to the invertebrate seedbank (resistance). Upon flow resumption, invertebrates can recolonise through aerial or aquatic dispersal (resilience).

actively or passively seek refuge in the hyporheic zone, where abiotic conditions are more stable (Wood et al., 2010). However, the use of hyporheic zones is conditioned by sediment characteristics, such as particle size that can filter out the larger taxa (Loskotová et al., 2019), and the traits of the taxa, such as size, form, and the physiological tolerance to interstitial water characteristics (Datry et al., 2007). If dry conditions persist, the water table can recede through the subsurface. In this case, aquatic invertebrates can only survive in damp streambed sediments as part of the 'invertebrate seedbank', which includes desiccation-tolerant life stages, such as dormant eggs and juveniles (Tronstad et al., 2005). Partially desiccation-tolerant taxa can also survive within the invertebrate seedbank, provided some sediment moisture remains (Loskotová et al., 2021; Stubbington et al., 2016). The survival of some taxa in the seedbank is linked to moisture content, although only a few can tolerate complete and extended dry phases (Bogan et al., 2015; Stubbington & Datry, 2013).

Resilience mechanisms are essential for maintaining populations of aquatic taxa that cannot persist *in situ* during drying (Bogan et al., 2017). Dispersal strategies are key to community recovery, as organisms can recolonise dry reaches when flow resumes (Chester & Robson, 2011; Pineda-Morante et al., 2022). Invertebrate dispersal among reaches includes different pathways, such as passive downstream drift, active aerial dispersion, and active swimming (Chester & Robson, 2011). Aquatic dispersers are restricted by hydrological connectivity, with drift dispersion being unidirectional from upstream perennial refuges to downstream intermittent reaches when flow resumes (Stubbington, Bogan, et al., 2017). By contrast, aerial dispersers can recolonise intermittent reaches from aquatic refuges in both directions of the same stream network or from nearby stream networks (Bogan et al., 2017). Insects in IRES may also adapt their life cycle to synchronise their different life stages with a suitable corresponding phase of IRES dynamics. For example, many Mediterranean IRES taxa show emergence peaks before seasonal drying and exhibit desiccation-tolerant life stages during the dry phase (Dolédec et al., 2017; López-Rodríguez et al., 2009).

The persistence of taxa in IRES requires traits that promote resistance, resilience, or both. Many taxa with varying resistance or resilience strategies can maintain populations in the network during the dry season due to sink-source dynamics (Sarremejane et al., 2021).For instance, *Pisidium* sp. clams, with low mobility to escape

or recolonise, are present in the seedbank as desiccation-tolerant life stages (Stubbington et al., 2016). At the network scale, resistance and resilience responses are not spatially coordinated, indicating heterogeneous responses along the network. This heterogeneity reflects the interactions of hydrological and climate drivers with local conditions (Leigh et al., 2016; Sarremejane et al., 2021). Thus, IRES communities are adapted to seasonal patterns, but how does the intensification of drying, along with other anthropogenic factors, impact the strategies used to face the dry phase?

Organic matter decomposition in IRES

The decomposition of organic matter (OM) is crucial for the functioning of stream ecosystems, playing a key role in biogeochemical cycles and serving as a reliable indicator of ecosystem functioning (Gessner & Chauvet, 2002; Swan et al., 2021). OM decomposition in IRES is influenced by various processes including leaching, microbial conditioning, and fragmentation induced by invertebrates and physical abrasion (Gessner et al., 1999). The dynamism of IRES, fluctuating between aquatic and terrestrial habitats, makes OM decomposition highly variable, being often viewed as 'pulsed biogeochemical reactors', where OM processing, storage, and transport fluctuate with the hydrological phases (Figure I.4; Larned et al., 2010).

During flowing conditions, OM decomposition in IRES is similar to that in perennial watercourses, being driven by a combination of abiotic (e.g., leaching of soluble compounds and physical abrasion) and biotic processes (e.g., microbial decomposition and breakdown by shredders) (Del Campo et al., 2021; Larned et al., 2010; von Schiller et al., 2017). However, as the flow decrease, the rate of OM decomposition declines, leading to accumulation on the riverbed and reduced OM transport, especially in IRES containing riparian areas with deciduous vegetation (Sanpera-Calbet et al., 2016; Steward et al., 2012).

Flow fragmentation creates a heterogeneous landscape of remnant pools within a matrix of dry streambeds, exposing OM to different environmental conditions. Local factors determine the water physicochemistry of remnant pools, with some pools acting as individual ecosystems characterized by distinct biogeochemical processes (Abril et al., 2016; von Schiller et al., 2017). For instance, isolated pools exposed to solar

radiation can become hypoxic due to increased temperatures and accumulated riparian leaf litter (Canhoto et al., 2013). On the other hand, pools connected to a hyporheic flow may become refuges for microbial decomposers and invertebrates (Bogan et al., 2017). With the complete disappearance of surface flow, dry streambeds become dominant in IRES, where OM accumulates due to reduced microbial and invertebrate activity (Abril et al., 2016). Moist habitats in dry streambeds, such as subsurface sediments, can still support some degree of OM decomposition through aquatic microbes (Abril et al., 2016; Arias-Real et al., 2020). Terrestrial invertebrates also play a role in OM processing during this phase, influenced by streambed characteristics, litter quality, and the dry-phase duration (Steward et al., 2017). Furthermore, in the absence of water, OM is susceptible to abiotic factors such as solar radiation (photodegradation), high temperatures, and occasional rainfall, impacting its quality (Steward et al., 2012). For instance, with a few days of dryness, the C:N ratio decreases, improving OM quality; however, long dry periods deteriorate OM quality (Datry et al., 2018). Upon flow resumption, aquatic decomposition is reactivated, and the downstream transport of OM is also triggered. The balance between decomposition and transport is influenced by the nature of rewetting; flash floods can lead to massive downstream transport, whereas gradual rewetting activates and favours microbial decomposition (von Schiller et al., 2017).

In the context of human-induced climate change, the increasing duration of dry phases in many natural IRES (Parmesan et al., 2022) is reducing the duration of flowing periods and the activity of aquatic biotic drivers. This results in more OM accumulating on dry streambeds and an increase in the transport of low-quality OM downstream, which could negatively impact detrital food webs and ecosystem functioning (Datry et al., 2018). Considering the importance of OM decomposition along the stream continuum and the spatiotemporal variability of flow conditions in IRES, a question arises: how does the processing of OM differ across an IRES network due to the variability of drying dynamics?

Biotic drivers

The main biotic drivers of aquatic OM decomposition in IRES are microbial decomposers and invertebrates (Webster & Benfield, 1986). Plant litter in streams is

rapidly colonised by microbial decomposers, which facilitate its consumption by shredders and other detritivores (Gessner et al., 1999; Graça, 2001). During dry phases, aquatic biotic drivers (microbes and invertebrates) are not active and terrestrial invertebrates can colonise the riverbed (Sánchez-Montoya et al., 2016), possibly contributing to the decomposition of the accumulated OM. However, evidence of this is still scarce (Del Campo et al., 2021).

Microbial decomposers

Microbial decomposers, including fungi and bacteria, are the first OM decomposers that contribute to the transfer of energy and nutrients to higher trophic levels in stream food webs (Romaní et al., 2017). They possess enzymes capable of breaking down structural molecules in plant litter, such as lignin and cellulose, which have slow breakdown rates (Webster & Benfield, 1986). Microbial decomposers enrich the quality of OM by incorporating dissolved nutrients from the water column (Suberkropp, 1998). While communities of bacteria alone show lower enzymatic activities, fungi are more efficient in processing structural molecules (Romaní et al., 2006). In addition, in terms of biomass and production, fungi surpass bacteria in breaking down coarse submerged

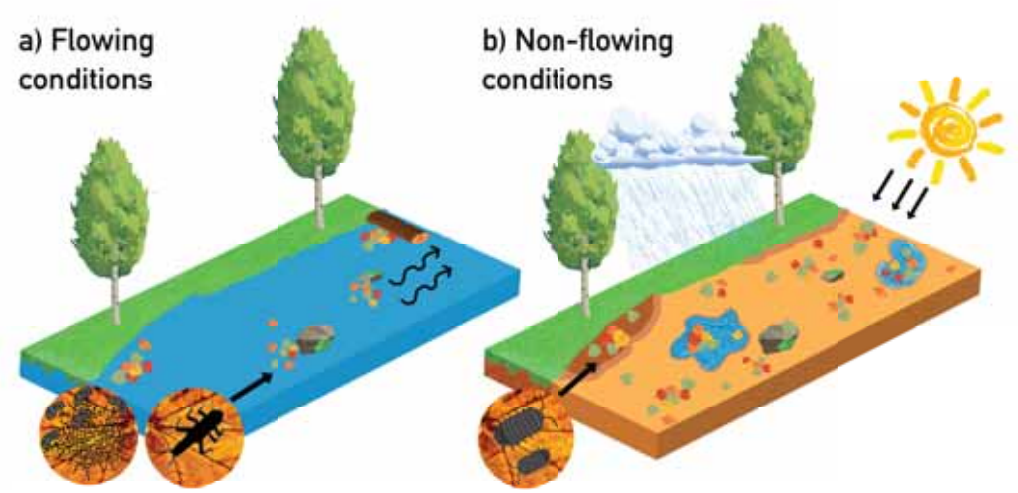


Figure I.4. OM decomposition in IRES: a) Under flowing conditions, OM decomposition resembles that in perennial watercourses, driven by a combination of abiotic (leaching and physical abrasion) and biotic factors (microbes and invertebrates); b) under non-flowing conditions, decomposition is primarily terrestrial, driven by mechanical abrasion and physical fragmentation. OM accumulates on the dry streambed and is susceptible to abiotic factors, such as solar radiation, high temperatures, and rainfall. Terrestrial invertebrates may also contribute to OM decomposition. Aquatic decomposition can persist in wet habitats (e.g., remnant pools and damp sediments). Adapted from Del Campo et al., 2021.

OM such as leaves and wood, whereas bacteria are more involved in processing fine OM and decaying floating-leaved macrophytes (Gessner et al., 2007). Overall, fungi are the primary decomposers of OM in freshwater systems, and there is a clear fungal succession during plant litter decomposition: when plant litter enters streams, terrestrial fungi tend to decline, favouring the contribution of aquatic fungi, particularly aquatic hyphomycetes (Gessner et al., 2007).

Aquatic hyphomycetes, consisting of 335 morphospecies (Duarte et al., 2016), are the most active fungal decomposers in streams and are a well-studied group of fungi (Bärlocher, 1992; Descals, 2005). They are well-adapted to the stream environment and produce different branched conidia that facilitate substrate attachment in flowing water, capturing and initiating the fungal colonisation of plant litter (Bärlocher, 1992; Dang et al., 2007; Descals, 2005). With the colonisation of plant litter, aquatic hyphomycetes directly degrade OM and enhance the palatability of the plant litter, stimulating the litter consumption by invertebrates (Gessner et al., 2007). Fungi transform inedible compounds into edible ones, decrease leaf toughness, and increase nutrient availability (Foucreau et al., 2013). This makes colonised plant litter a better resource for invertebrate consumption (Graça, 2001). Moreover, fungi can obtain nutrients from both the substrate and the surrounding water (Suberkropp, 1998).

As key aquatic decomposers of plant litter, the biomass and reproduction of fungi are directly related to aquatic decomposition rates (Gessner & Chauvet, 1994) and are affected by the same abiotic and biotic factors such as litter quality (Fernandes et al., 2012), competitive interactions between fungal species (Fryar et al., 2005), competitive interactions with bacteria (Gulis & Suberkropp, 2003), temperature (Geraldes et al., 2012), nutrient concentrations in water (Ferreira & Graça, 2016), oxygen concentration (Medeiros et al., 2009), pollutants (Moreirinha et al., 2011), and flow regime (Arias-Real et al., 2023).

Invertebrates

The invertebrates associated with plant litter, mainly shredders (which rip and shred leaves during feeding), are predominantly represented by insects from different orders such as Plecoptera, Trichoptera, and Diptera (Graça, 2001). Shredders play an important role in detrital food webs and are driven by the availability of allochthonous

organic inputs (Cheshire et al., 2005). The main role of invertebrates in plant litter decomposition is the transformation of coarse particulate OM, such as leaves and wood, into fine particulate OM through fragmentation (Gessner et al., 1999). This role facilitates the decomposition of terrestrial litter inputs and enhances the availability of litter resources for other invertebrates (e.g., collector gatherers or collector filterers). At the same time, their excretions constitute an important pre-processed resource for other organisms such as microbes (Villanueva et al., 2012). Shredders are present in all types of freshwater systems, but their importance is greater in ecosystems receiving seasonally large inputs of litter. Therefore, their life cycles are often related to seasonal pulses in resource availability and they can exhibit a certain plasticity in their feeding habits by acting as scrapers or collectors (Jonsson & Sponseller, 2021).

Shredders are selective feeders, that are influenced by the toughness of the litter, the nutrient content (especially nitrogen), and the presence of secondary plant components (Danger et al., 2012; Irons et al., 1988). Consequently, litter conditioned by hyphomycetes is preferred by these invertebrates due to the benefits of fungal action on the litter. Moreover, the invertebrates can also feed directly on the fungi. However, shredders are affected by variations in biotic and abiotic factors such as species interactions (Dangles & Malmqvist, 2004), nutrient concentrations in water (Heino, 2000), water temperature (Mas-Martí et al., 2015), flow level (Mustonen et al., 2016), current velocity (Cristiano & Di Sabatino, 2023), the presence of pollutants (Carlisle & Clements, 2005), and substrate type (Milesi et al., 2016), which all influence community species composition.

Land uses in IRES

In recent decades, numerous studies have highlighted the extent of changes in land uses worldwide, primarily driven by anthropogenic activities. Such transformations can alter and potentially degrade stream habitats (Allan, 2004). Land use intensification impacts riparian vegetation, stream morphology, and water chemistry, subsequently affecting biodiversity and ecosystem functioning in stream networks (Carpenter et al., 2011). Land use intensification reduces multiple components of stream biodiversity across the scales, with urban and agricultural streams showing the most pronounced

effects (Petsch et al., 2021). However, these impacts are not uniformly distributed along the network, displaying spatial heterogeneity due to physical and chemical differences. This variation affects the diversity of resources and refuges for organisms along the river channel (Barboza et al., 2015). For instance, in an agricultural gradient in a river network, the sections less impacted by agriculture host a higher number of sensitive taxa compared to the more affected areas, with species abundances also fluctuating (Baumgartner & Robinson, 2017). Despite the extensive literature on the effects of land use intensification, most studies primarily focus on comparing ecosystem functioning or diversity on a small scale, typically at the reach scale. Understanding precisely how biodiversity shifts in a changing landscape requires the examination of multiple components of biodiversity change across several spatial scales (Petsch et al., 2021).

In IRES, the natural gradient of flow variability varies with anthropogenic landscape gradients (Chiu et al., 2017). Only a few studies have focused on the effects of land use intensification and drying on biodiversity and ecosystem functioning (but see Grantham et al., 2012; Reid et al., 2013; Theodoropoulos et al., 2015). For instance, Theodoropoulos et al. (2015) identified agriculture as the predominant factor affecting the distribution of invertebrates, especially sensitive taxa, with drying primarily reducing invertebrate density. Reid et al. (2013) found that agricultural land uses, combined with drying, can produce cumulative effects that are not mitigated by riparian vegetation.

Natural areas in IRES

Natural areas comprise lands predominantly covered by natural vegetation that are largely free from human activities, such as forests and shrublands. In freshwater systems, the land cover of drainage catchments and their associated riparian zones highly influence the quality of streams and physical habitats (England & Rosemond, 2004). For instance, forests modulate drainage and surface runoff into streams by interacting with variables like evapotranspiration, soil moisture, and precipitation (Oishi et al., 2010). Concurrently, riparian forests counteract erosion with tree roots stabilising stream banks, linking terrestrial and aquatic environments. They also enhance the chemical quality of stream water by retaining nutrients, pesticides, and

other pollutants (Broadmeadow & Nisbet, 2004). Within streams, wooden substrates fulfil varying roles, from habitat provision to flow pattern alteration (Williams & Morris, 2005). Forest canopies modulate the sunlight incidence, thereby regulating the riparian microclimate and primary production. In addition, vegetation is an essential energy source for many stream ecosystems (Vannote et al., 1980). In this context, forested watersheds generally ensure superior water quality, aquatic habitats, and recreational opportunities (Schoenholtz, 2004).

In the Mediterranean, intensive agriculture and urban development occur mainly in the plains, while natural areas are located at higher elevations (Sirami et al., 2010). Forests in mountainous areas are important for the supply of ecosystem services, such as carbon sequestration and fodder production, and they also host headwater streams with a high conservation value (Portela et al., 2021). In most Mediterranean streams, headwaters are located in mountainous areas (Cooper et al., 2013). Headwater streams are important to the ecology and biological integrity of downstream areas, as they represent up to 80% of stream networks, with the flowing water providing a continuous source of essential resources such as nutrients and OM (Wipfli et al., 2007). Headwater streams provide habitats for a diverse array of species, enhancing the biological diversity of the entire river network and serving as refuges or sources of colonists (Meyer et al., 2007).

Headwater streams play a key role in linking terrestrial and aquatic ecosystems and influencing the quality of downstream water (Dodds & Oakes, 2008; Heinz et al., 2015). For example, headwater streams draining forest catchments largely rely on leaf litter inputs from adjacent terrestrial ecosystems, which are crucial in supporting aquatic food webs throughout the stream network (Danger et al., 2021). However, increased evapotranspiration in forested areas can affect flow and surface runoff, with decreases correlating with increases in forested areas (Barrientos et al., 2020; Gallart & Llorens, 2004). In the Mediterranean region, where water scarcity is common, mountainous regions supply water, but transitions from agricultural lands to forested regions can reduce surface runoff (Delgado et al., 2010). Specifically, in this region, the expansion of forest cover – attributable to land abandonment and aggravated by human-induced climate change such as temperature increases and changes in rainfall patterns – in combination with growing human water demand may reduce streamflow.

Given these factors, can natural areas in the Mediterranean IRES network serve as a buffer against the effects of natural drying on ecosystem functioning and diversity?

Human landscapes: agricultural land uses

Human activities profoundly transform landscapes, invariably affecting the biodiversity and functioning of ecosystems worldwide (Arnet et al., 2022). IRES face threats similar to those encountered by perennial watercourses, such as changes in geomorphology and water quality. Yet, IRES receive comparatively less protection and attention, rendering them potentially more susceptible to degradation than perennial systems (Chiu et al., 2017).

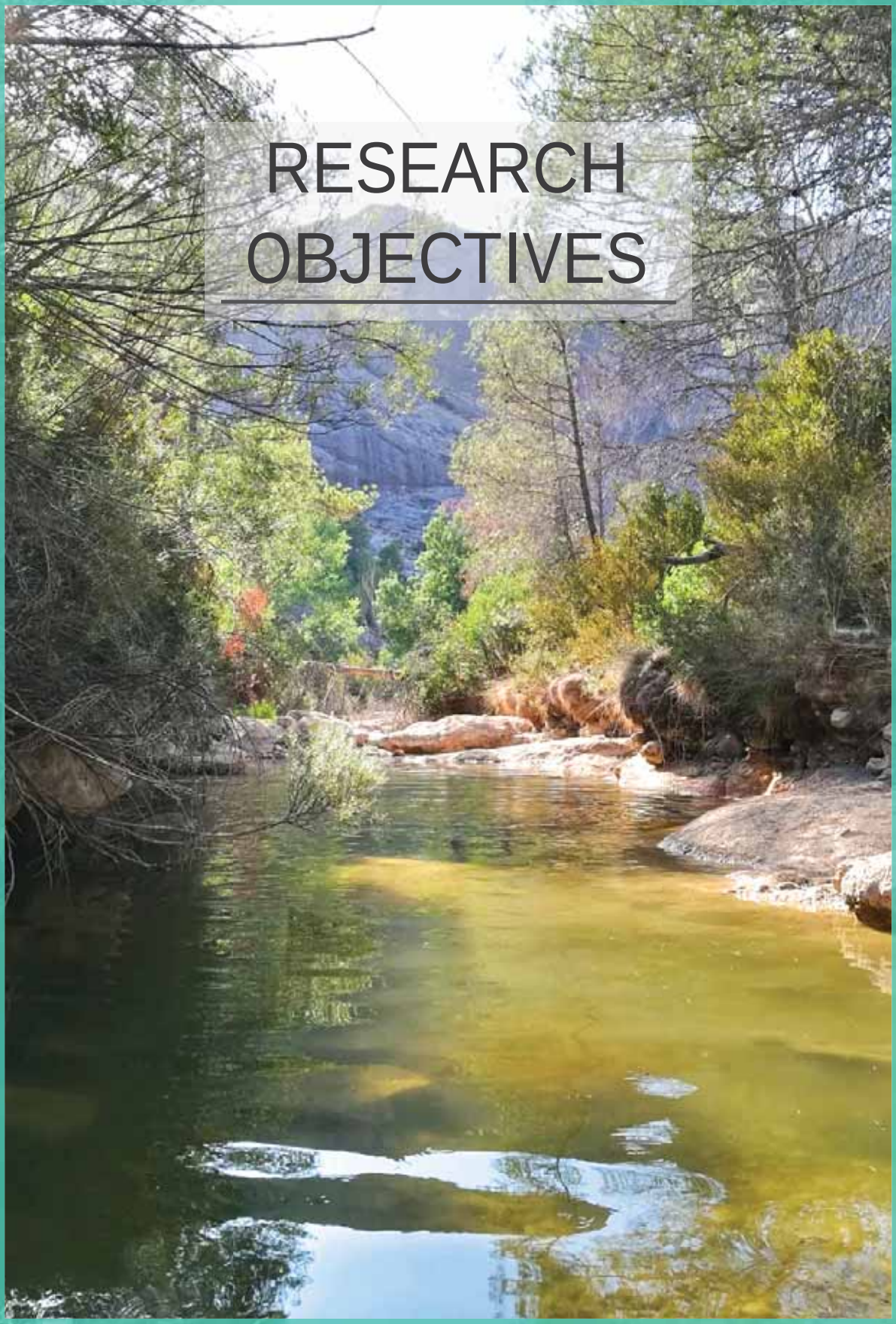
The intensification and expansion of agriculture during the 20th century have reshaped the landscape, precipitating habitat degradation (Helms et al., 2009). This agricultural impact manifests in diverse ways: alterations in water chemistry, degradation of soil and riparian zones, promotion of channelisation, and modifications in hydrological cycles. Furthermore, intensified agriculture correlates with an increased nutrient enrichment of water, particularly with nitrate and phosphorus (Jarvie et al., 2010; Lassaletta et al., 2009). Notably, nutrient enrichment accounts for nearly 35% of the variance observed in the ecological status of European waters, with these nutrients often interacting with toxic substances such as pesticides (Lemm et al., 2021). Moreover, the removal of riparian vegetation and soil degradation accelerate sediment loading in water due to soil erosion (Alberto et al., 2016). Agriculture also impacts hydrological cycles through water extraction and changes in evapotranspiration rates, which, in turn, affect surface runoff and river flow (Rideout et al., 2022).

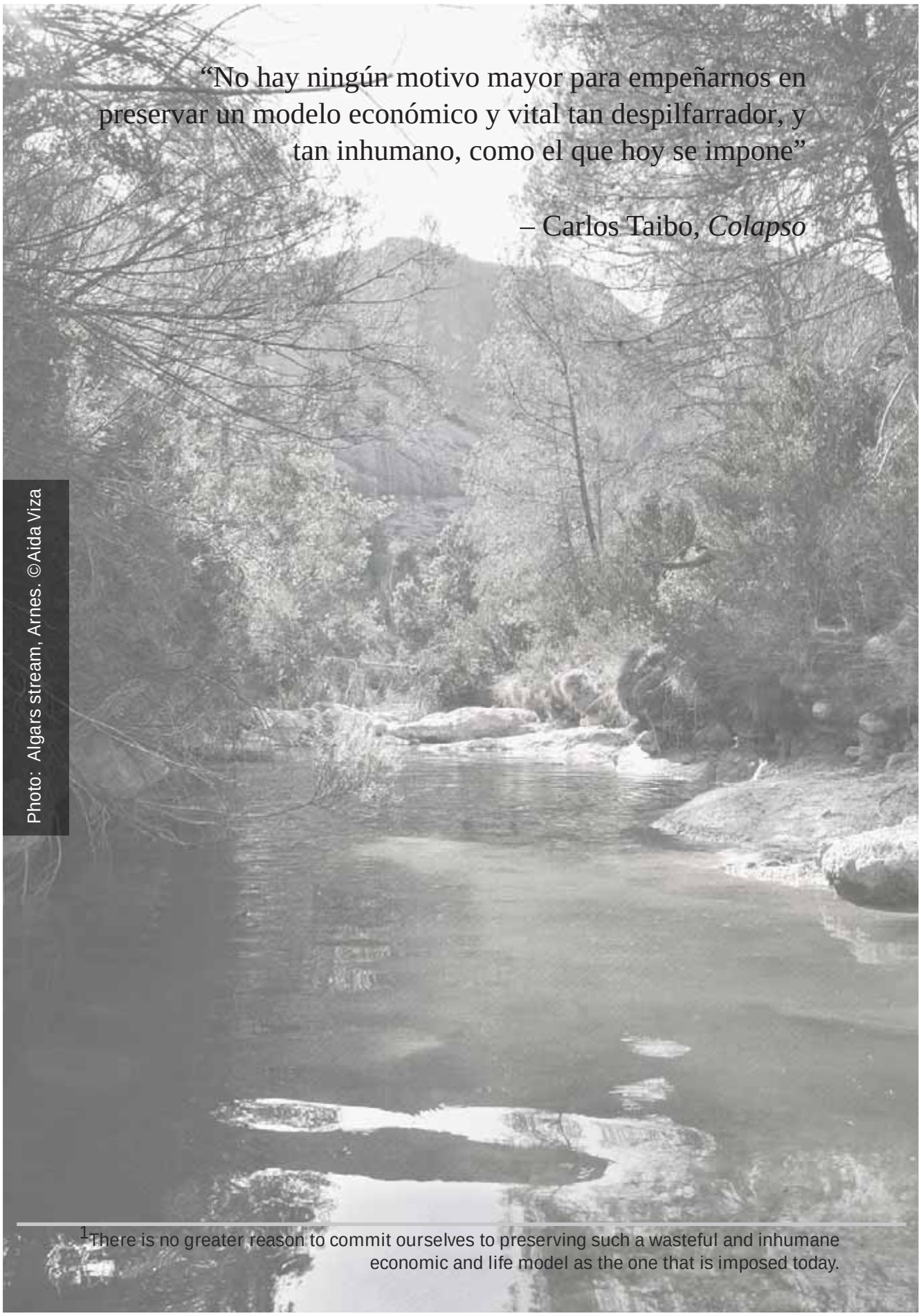
Habitat degradation can increase the local abundance or regional distribution of invasive species (Hermoso et al., 2011). Additionally, the taxonomic composition of consumers (e.g., invertebrates and fish) in agricultural watersheds tends to homogenise, marked by the loss of sensitive taxa and the proliferation of generalist taxa (Johnson & Angeler, 2014). While primary production might surge due to nutrient enrichment and increased light exposure (Frankforter et al., 2010), this often results in eutrophication and consequent alterations in the food web (Dodds & Smith, 2016). Agriculture also affects OM decomposition, enhancing nutrient availability for

microbial decomposers, altering litter inputs within the stream channel, and reducing the presence of shredders in open-canopy areas (Hladyz et al., 2011). Thus, habitat degradation emerges as a leading and persistent driver of biodiversity decline in freshwater systems in agricultural landscapes (Reid et al., 2019).

A pivotal question thus arises: how does the interplay between different levels of both agriculture and drying influence biodiversity and ecosystem functioning in a network of IRES, especially with seasonal flow variability?

RESEARCH OBJECTIVES





"No hay ningún motivo mayor para empeñarnos en preservar un modelo económico y vital tan despilfarrador, y tan inhumano, como el que hoy se impone"

– Carlos Taibo, *Colapso*

Photo: Algars stream, Arnes. ©Aida Viza

[1] There is no greater reason to commit ourselves to preserving such a wasteful and inhumane economic and life model as the one that is imposed today.

Research Objectives

This thesis focuses on the effects of the interplay between drying and land uses on diversity and ecosystem functioning in a Mediterranean stream network. Specifically, I study the influence of drying and agricultural activities on OM decomposition and aquatic communities (mainly on fungi and invertebrates) across an intermittent stream network during a hydrological year. Additionally, this work explores the mechanisms of *in situ* persistence (resistance) employed by benthic invertebrates, aiming to elucidate community recovery dynamics with flow resumption. The primary content of this thesis is structured into three chapters, each written as an independent publication. Chapters 1 and 3 centre on the Algars stream network (Figure O.1), a small intermittent stream with forested headwaters and agricultural activities occurring throughout the network. Chapter 2 examines six sites from various streams with differing durations of dry phases, including the Algars stream. The findings in this chapter are at the reach scale and additional data from mesocosm experiments are incorporated (Figure O.2). The specific objectives for each chapter are as follows.

In Chapter 1, I evaluate the effects of drying and agriculture on diversity at the stream network scale, using invertebrates that were seasonally collected during a hydrological year. This includes both taxonomic and functional dimensions, based on traits associated with strategies to cope with drying and nutrient-enriched water. The following is assessed: (i) differences in taxonomic and functional α-diversities due to variations in drying and agriculture throughout the network; (ii) the mechanisms by which these factors produce changes in taxa and trait composition; and (iii) the effects of drying on the temporal fluctuation of β-diversity. I identify the main environmental factors affecting the diversity metrics, as well as the trait and species compositions. I hypothesize that drying and agriculture will negatively affect α-diversity due to the loss of taxa sensitive to desiccation and pollution, respectively, impacting taxa and trait composition and affecting temporal changes in β-diversity, which are anticipated to be higher in the drying reaches than in those affected by agriculture.

In Chapter 2, I explore the contributions of hyporheic refuges and invertebrate seedbanks to the persistence of benthic aquatic invertebrates *in situ* during dry phases

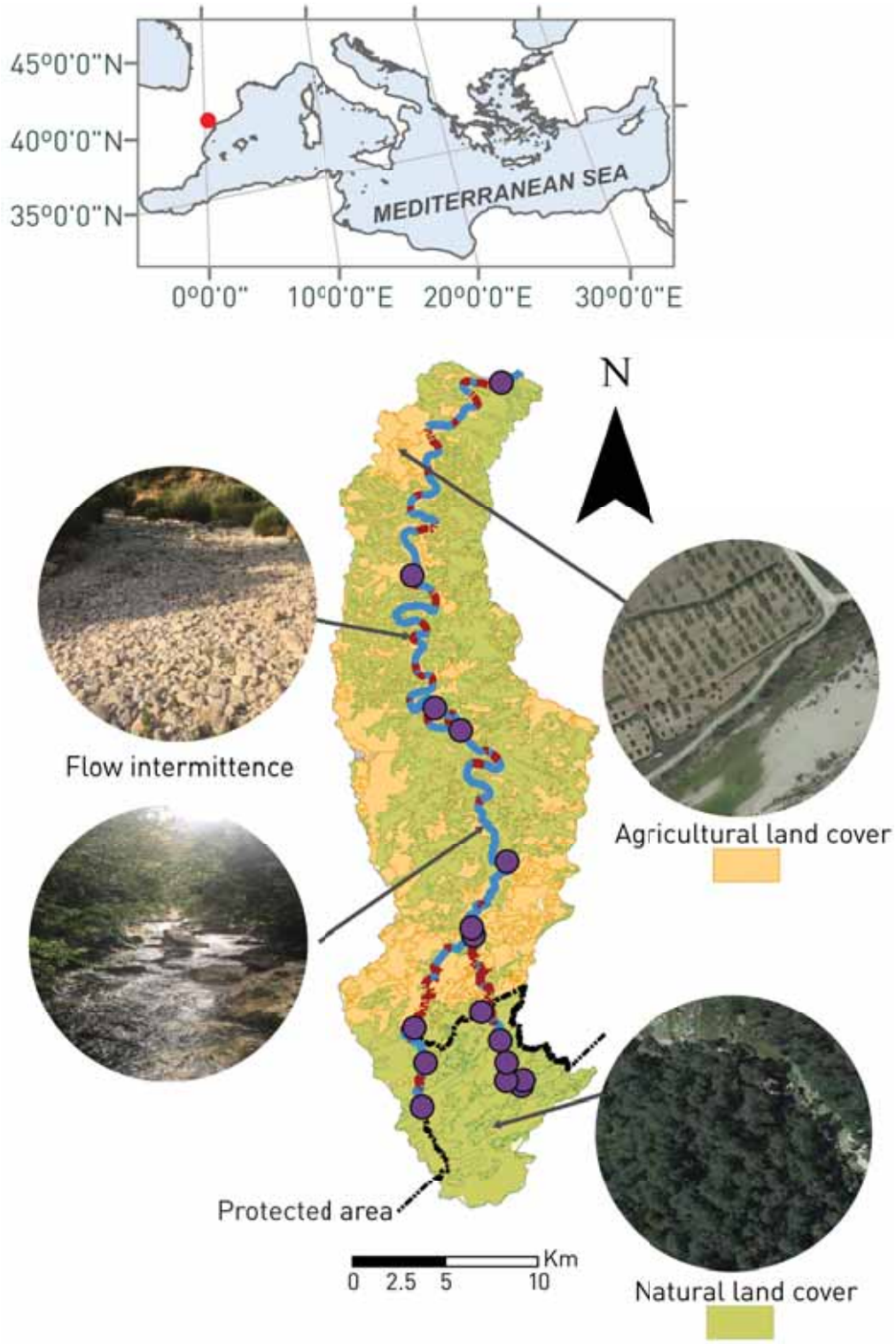


Figure 0.1. The Algars stream network, delineating the reaches sampled. The type of land cover is indicated by different colours. The colour gradient of the stream also signifies flow intermittency levels.

at the reach scale. This will use information from the invertebrates collected during the dry phase from the hyporheic zones of six different intermittent reaches as well as from the dry sediments of the dry streambeds from the same reaches. The assemblages from these samples are compared with those from benthic samples collected during flowing conditions. Specifically, I characterize taxonomic and functional diversities and the relative abundances of traits related to the resistance and resilience to dry phases, aiming to assess: (i) differences in taxonomic and functional diversities between benthic assemblages and those in hyporheic refuges and seedbanks; (ii) differences in the relative contribution of traits related to the resistance to dry phases in each assemblage; and (iii) the effects of dry-phase duration on taxonomic and functional diversities. I hypothesize that hyporheic and seedbank assemblages will be subsets of benthic assemblages, but some traits related to the resistance to dry phases will be more abundant in hyporheic and seedbank assemblages than in benthic ones. Additionally, extended dry phases will be expected to reduce functional and taxonomic diversities, but the abundance of traits related to the resistance to dry phases will increase.

In Chapter 3, I analyse the effect of drying and land uses on ecosystem functioning at the stream network scale, using wood decomposition as a functional indicator. Specifically, I examine the differences in wood decomposition along the Algars stream network during a hydrological year. I aim to elucidate: (i) the effects of drying on ecosystem functioning and (ii) their interaction with the effects of land use. To explain the variability across the stream network, I identify the main environmental factors affecting the decomposition rates and their primary drivers (aquatic fungi). I hypothesize that with a high intensity of the dry phase, wood decomposition and fungal biomass will decrease, but agriculture will partially buffer this negative effect.

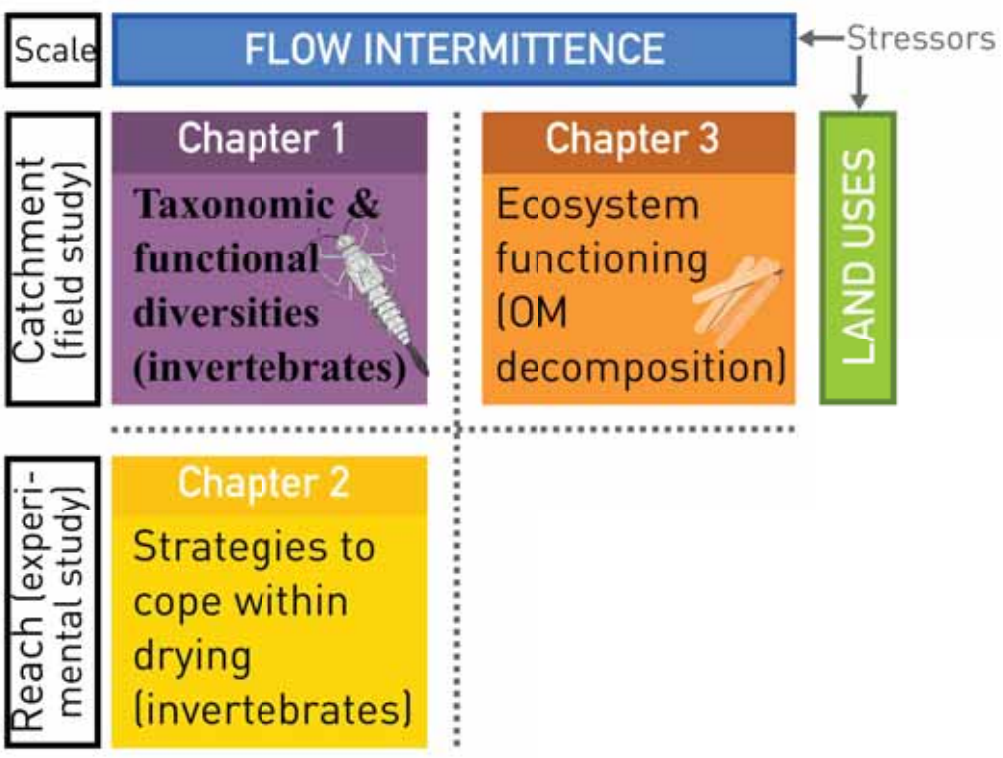
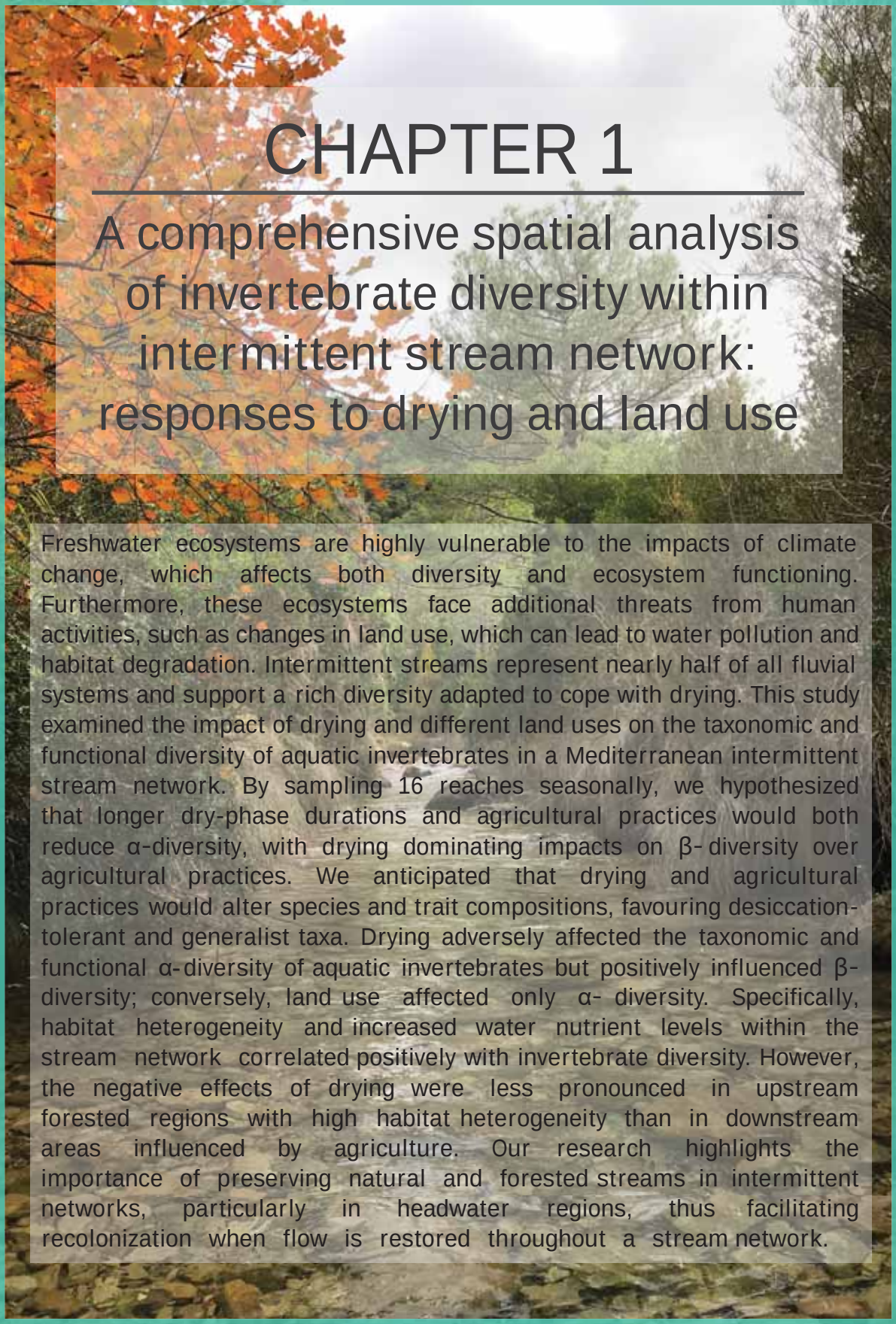


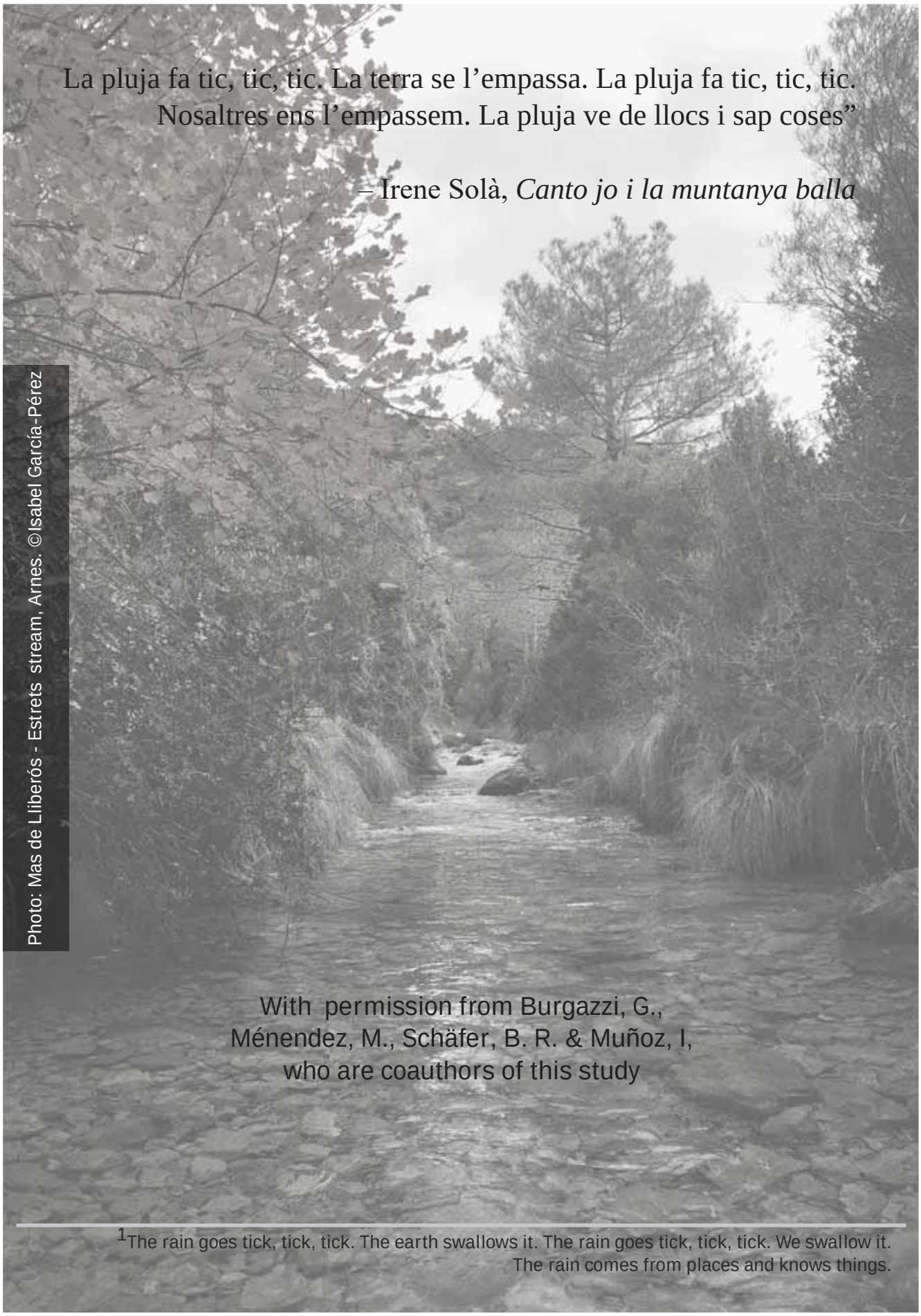
Figure 0.2. Scheme of the objectives of this thesis. Chapters 1 and 3 utilise field data from the Algars stream network (Figure O.5), focusing on the catchment scale. Chapter 2 combines field data with data from mesocosm experiments, focusing on the reach scale. All chapters investigate the effects of drying, while Chapters 1 and 3 also evaluate the effects of land use.



CHAPTER 1

A comprehensive spatial analysis of invertebrate diversity within intermittent stream network: responses to drying and land use

Freshwater ecosystems are highly vulnerable to the impacts of climate change, which affects both diversity and ecosystem functioning. Furthermore, these ecosystems face additional threats from human activities, such as changes in land use, which can lead to water pollution and habitat degradation. Intermittent streams represent nearly half of all fluvial systems and support a rich diversity adapted to cope with drying. This study examined the impact of drying and different land uses on the taxonomic and functional diversity of aquatic invertebrates in a Mediterranean intermittent stream network. By sampling 16 reaches seasonally, we hypothesized that longer dry-phase durations and agricultural practices would both reduce α-diversity, with drying dominating impacts on β- diversity over agricultural practices. We anticipated that drying and agricultural practices would alter species and trait compositions, favouring desiccation-tolerant and generalist taxa. Drying adversely affected the taxonomic and functional α-diversity of aquatic invertebrates but positively influenced β-diversity; conversely, land use affected only α- diversity. Specifically, habitat heterogeneity and increased water nutrient levels within the stream network correlated positively with invertebrate diversity. However, the negative effects of drying were less pronounced in upstream forested regions with high habitat heterogeneity than in downstream areas influenced by agriculture. Our research highlights the importance of preserving natural and forested streams in intermittent networks, particularly in headwater regions, thus facilitating recolonization when flow is restored throughout a stream network.



La pluja fa tic, tic, tic. La terra se l'empassa. La pluja fa tic, tic, tic.
Nosaltres ens l'empassem. La pluja ve de llocs i sap coses"

– Irene Solà, *Canto jo i la muntanya balla*

Photo: Mas de Liberós - Estrets stream, Arnes. ©Isabel García-Pérez

With permission from Burgazzi, G.,
Ménendez, M., Schäfer, B. R. & Muñoz, I,
who are coauthors of this study

[1]The rain goes tick, tick, tick. The earth swallows it. The rain goes tick, tick, tick. We swallow it.
The rain comes from places and knows things.

INTRODUCTION

Freshwater systems are among the ecosystems most threatened by human-induced climate change, which affects freshwater diversity and ecosystem functioning (Parmesan, Camille et al., 2023). Consequently, the global distribution and extent of intermittent rivers are changing. Comprising almost 50% of the global river network, intermittent watercourses are found in all climates, biomes, and continents (Messager et al., 2021). Although natural intermittent streams experience periodic flow interruption, the frequency and intensity of these interruptions have increased in recent decades due to anthropogenic alterations to hydrological regimes and regional water scarcity, increasing the spatial and temporal extension of flow intermittency and intensifying and prolonging dry periods (Datry et al., 2016).

Typically, flow interruption occurs irregularly across an intermittent stream network, creating a dynamic mosaic of wet and dry sections spatially and temporally (Datry et al., 2014). Intermittent streams are common in Mediterranean climates and are characterized by seasonal and predictable dry and wet periods (Bonada & Resh, 2013). Between late spring and early summer, the flow gradually decreases, leading to the formation of isolated pools by flow fragmentation, and depending on the intensity and duration of drying, the total dry-up of the streambed occurs. At the end of summer or in early autumn, rewetting usually occurs quickly due to heavy rainfall events, although it is sometimes re-established more gradually through a decrease in evapotranspiration and an increase in the groundwater level (Costigan et al., 2017).

Natural intermittent stream networks support high diversity and are adapted to cope with a certain level of drying (Bogan et al., 2017). The natural variability of intermittent streams results in temporal and spatial changes in α- and β-diversity across the stream network, as species in these streams exhibit traits such as aerial respiration or aerial dispersal ability, which promote their survival through strategies of either resistance or resilience (Bogan et al., 2017). For instance, at the reach scale, when flow disruption begins, macroinvertebrates characteristic of lentic pools replace lotic taxa through turnover (Bonada et al., 2006). The progression of drying leads to the disappearance of rheophilic and desiccation-sensitive taxa, reflecting a nestedness

process (Stubbington et al., 2017) and negatively affecting α-diversity (Arias-Real et al., 2021). At the reach scale, when the water table recedes and the streambed dries, aquatic taxa can persist only in hyporheic refuges or as part of the invertebrate seedbank (Robson et al., 2011). However, increases in the intensity and extension of drying events can compromise the viability of *in situ* survival strategies (Crabot, Mondy, et al., 2021), as well as the persistence of perennial reaches, one of the sources of colonizers, becoming intermittent (Gill et al., 2022).

Intermittent stream networks have been both directly and indirectly impacted by changes in human activities in recent decades (Datry et al., 2018). For instance, the intensification of agriculture strongly influences water quality through the enrichment of water nutrients, particularly inorganic N and P concentrations, as well as pesticide pollution (Carpenter et al., 2011; Liess et al., 2021). Moreover, agricultural intensification leads to habitat destruction and increased water demand, which in turn influences hydrology (Allan, 2004). These factors affect aquatic diversity, resulting in alterations in taxa and trait composition (Pallottini et al., 2017). For instance, in reaches impacted by agriculture, generalist taxa typically increase in abundance, leading to reductions in both functional and taxonomic diversity (Lange et al., 2014). However, the specific effect of agriculture on invertebrate composition depends on stressor intensity (Piscart et al., 2009), and agricultural activity can positively influence the abundance or richness of invertebrates (Jähnig et al., 2021; van Klink et al., 2020). However, the impacts of agriculture on intermittent stream communities have been less studied, especially when evaluating entire stream networks and spatial distributions during drying (but see Cid et al., 2022; Datry et al., 2023). Specifically, the communities in reaches with a high prevalence of agricultural activities paired with lower discharge, complete disconnection or dry out may be the most adversely affected.

The aim of this study was to analyse the changes in the taxonomic and functional diversities of aquatic invertebrate assemblages across an intermittent stream network under a Mediterranean climate with respect to different degrees of drying intensity and land use. To achieve this goal, we selected 16 sites within a small stream network and collected macroinvertebrate samples seasonally over the course of a hydrological year. Specifically, we hypothesize that (1) sites with longer drying periods or those affected by agriculture, expressed as nutrient water enrichment, will exhibit lower

taxonomic and functional α-diversities due to the disappearance of desiccation- or pollution-sensitive taxa; (2) this translates into shifts in the taxa and trait compositions towards desiccation-tolerant life stages and generalist taxa; and (3) temporal changes in β-diversity will be greater in drying sites than in agriculturally impacted reaches owing to desiccation-induced nestedness processes affecting sensitive taxa (Rolls et al., 2023).

MATERIALS AND METHODS

Study area and site selection

This study was conducted in the Algars stream network, which is located in the northeastern part of the Iberian Peninsula. It flows into the Matarranya River, a tributary of the Ebro River (Figure 1.1). The stream network encompasses a total catchment area of 405 km^2 and features a 70 km long mainstream. The Algars headwaters comprise two streams, Estrets and Algars, both of which are located mainly in the natural park of Els Ports. The region's climate is typically Mediterranean, characterized by scarce precipitation concentrated in spring and autumn and drier and warmer summers. Extensive agriculture, predominantly olive groves, fruit trees, and vineyards, covers 44.6% of the catchment area. The natural cover, which includes coniferous forests, bare rocks, sclerophyllous vegetation, and transitional woodlands–shrubs, constitutes 55.3% of the catchment area. Urban land use is minimal, accounting for less than 0.45% of the area (Corine Land Cover, 2018). For this study, we selected 16 sites across the catchment: seven on the Estrets stream (headwaters), three on the Algars stream (headwaters), and six on the Algars mainstream after the confluence (Figure 1.1). The two last reaches in each headwater stream, A3 and E16, were located outside of the Natural Park. This study spanned a hydrological year, from November 2018 to November 2019, during which the basin received a total of 368.9 mm of cumulative precipitation (Meteorological Service of Catalonia, METEOCAT).

Macroinvertebrate sampling and trait data collection

We conducted four seasonal samplings at each site and collected macroinvertebrate samples using a 250-µm mesh. At each site and during each

sampling occasion, we collected a total of five replicate samples from different riffle and shallow zones using a Surber sampler, provided that the flow was connected. In cases where disconnected pools occurred in any of the reaches, we collected three-minute kick samples with a 250-μm net following a standardized multihabitat protocol that represented each habitat in proportion to its occurrence (Jáimez-Cuéllar et al., 2002).

All invertebrates were identified to the genus level following Tachet et al. (2010), except for Diptera (which were identified to the subfamily or family level), Oligochaeta

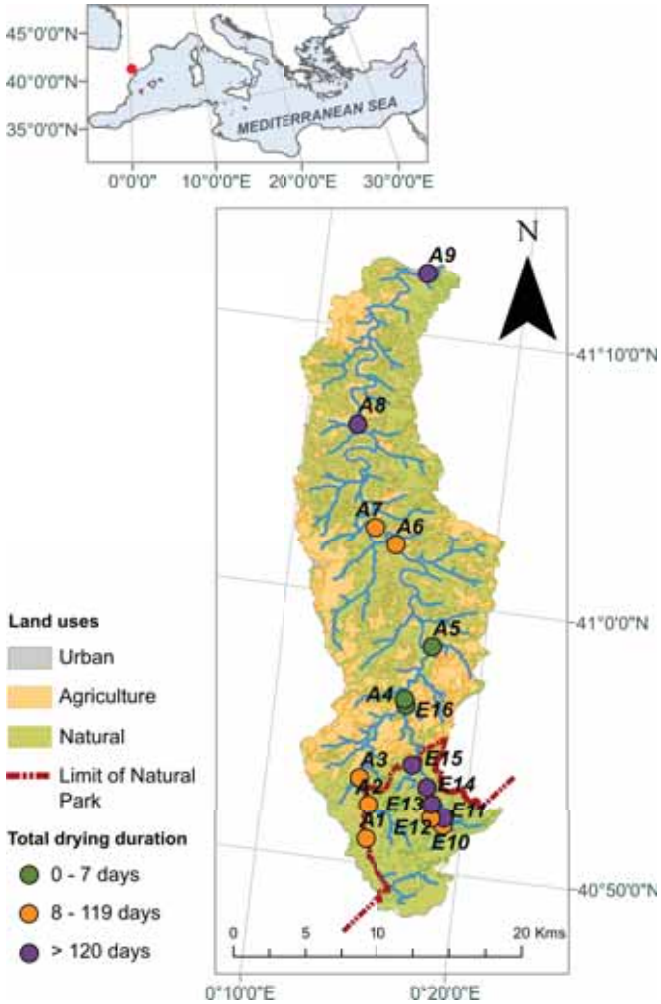


Figure 1.1. Location of the Algars stream network in the Mediterranean basin and the site locations (points) inside the stream network. The background of the map is coloured according to land use: grey, urban; orange, agricultural; and green, natural. Points are coloured according to total dry-phase duration during the whole study period: green, permanent (0–5 days); orange, low and medium (6–119 days); and lilac, high (> 120 days).

(identified to the subclass level), Nematoda (identified to the phylum level), and individuals that were too small for accurate identification. Because various sampling methods were employed and to facilitate comparisons between reaches, we pooled the replicates within each site and calculated the relative abundances of all the taxa.

To explore trait composition, we selected traits related to strategies to cope with drying (i.e., drying traits) and to cope with nutrient-enriched water from two different databases (Múrria et al., 2020; Sarremejane, Cid, et al., 2020). The selected traits included maximum body size, life cycle duration, potential number of reproduction cycles per year, reproduction type, resistance forms, respiration type, locomotion, and propensity to drift. All traits were codified using a fuzzy code approach (Chevenet et al., 1994), and category scores were standardized to proportions by setting their sum to 1. Our final trait set included 30 categories belonging to 9 traits (Table S1.1).

Stream flow intermittency assessment

To characterize drying, we installed leveloggers (Solinst Levelogger Edge, with a full-scale reading accuracy of 0.05%) on the streambed at each site to measure the water level and daily streambed temperature variation as an indicator of water presence throughout a hydrological year. To correct the recorded data, we used atmospheric pressure variations obtained from barologgers (Solinst Barologger, full-scale reading accuracy of 0.05%) installed in the riparian zone of each site (Constantz et al., 2001). We calculated the total number of days without water (DD, dry-phase duration) and the total number of periods without water (DF, drying frequency) during the three months prior to each sampling occasion at each site.

Environmental parameters

During the study period, physical and chemical parameters were seasonally measured at each site. At each sampling occasion, a portable probe (YSI Professional Plus Multiparameter Instrument, USA) was used *in situ* at each site to measure electrical conductivity, water temperature, water dissolved oxygen, and pH (±1 µS cm−1, ± 0.1 °C, ± 0.1 mg L−1 and ± 0.005 pH, respectively). However, water temperature and oxygen concentration were excluded due to inconsistent collection times affecting daily temperature variation. To characterize the water nutrient concentrations, three

water samples were filtered through glass fibre filters (0.7 μm pore size; Whatman GF/F, Germany) into prewashed polyethylene containers, transported to the laboratory and stored at 4 °C in the dark until analysis. Water samples were analysed for dissolved inorganic nitrogen (DIN) (nitrite, nitrate, ammonium) by ionic chromatography (± 2.8% at 1 ppm; IC5000, DIONEX, USA) and for dissolved organic carbon (DOC) by a TOC analyser (TOC-V CSH, Shimadzu Corporation, Japan).

To characterize land use, we delineated the subbasin of each site using a digital elevation model with a resolution of 25 m, computing the flow direction and applying a watershed tool with geospatial processing software (ArcMap 10, ArcGIS, USA). We simplified the categories of land-use cover to urban, natural, and agricultural land uses, adapted from Corine Land Cover (2018).

Additionally, we used a spherical densitometer (Lemmon, 1956) to calculate the average canopy cover percentage at each site, taking four measurements (upstream, downstream and right and left sides of the site) at three points for each site. The riparian quality and fluvial habitat indices adapted to Mediterranean streams (QBR and IHF, respectively) were calculated at each site and time (Table S1.2) (Munné et al., 2003; Pardo, 2002).

Statistical analyses

Environmental exploration and variable selection

We explored the relationships between environmental variables for collinearity using Spearman correlation and bivariate scatter plots and selected variables with correlation coefficients less than 0.50. Multicollinearity was further assessed using the variance inflation factor (VIF) function of the usdm R package (Naimi et al., 2014). For subsequent analyses, we selected DD, DOC, and DIN concentrations; water conductivity; and the IHF index, treating the DIN concentration as an indicator of agricultural land use due to its high correlation with this variable (0.70). DIN, DD, and DOC were square root-transformed to approximate a normal distribution because these variables exhibited a very skewed distribution.

To check for independence of the sites in the stream network, we employed empirical variograms to evaluate the spatial autocorrelation of the selected variables

(Calder & Cressie, 2009) using the *GStat* R package (Gräler et al., 2016; Pebesma, 2004). None of the variables exhibited spatial correlation (Figure S1.1).

Diversity metrics

For taxonomic α-diversity, we calculated the Shannon–Wiener index (H'), taxonomic richness (S), and Ephemeroptera–Plecoptera–Trichoptera index (EPT) using the *vegan* R package (Oksanen et al., 2022). For functional α-diversity, functional richness (FRic) and functional redundancy (FRed) were calculated. FRic was determined as the minimum hypervolume of functional space occupied by a set of invertebrates (Villéger et al., 2008). The functional space, encompassing all taxa and traits, was constructed using a Gower dissimilarity trait matrix. This analysis was carried out through a principal coordinates analysis (Múrria et al., 2020) conducted using the *ade4* R package (Dray & Dufour, 2007). FRed was defined as the difference between the Simpson index of taxonomic diversity and Rao's quadratic entropy (de Bello et al., 2007). FRed is the degree of functional equivalence among species within an ecosystem and refers to the situation in which one specific ecological function can be carried out by one or multiple species (Naeem, 2008).

To analyse changes within the community, we calculated temporal taxonomic and functional β-diversity metrics (TβD and FβD, respectively) at each site using Sørensen family indices. These were partitioned into species replacement ($\beta_{Replacement}$) and richness difference ($\beta_{Richness}$) components (Cardoso et al., 2014). For the taxonomic data, we employed a presence/absence-based approach using the *adespatial* R package (Dray et al., 2022). For the trait data, we computed the taxon Gower's distance matrix (Gower, 1971) and subsequently generated a dendrogram using hierarchical clustering analysis, which employed Ward's algorithm. The final step of calculating the functional β-diversity was carried out using the "beta" R function of the *BAT* package (Cardoso et al., 2022).

Statistical analyses

To analyse the effects of environmental factors and dry-phases on diversity metrics, we constructed linear mixed models (LMMs) using diversity metrics as response and environmental factors and dry-phases and seasons as predictors. Stream reach was used as a random factor. To determine the best-performing LMMs, we employed a top-

down approach for model evaluation and selection (Zuur et al., 2009). Model selection was based on the Akaike information criterion (AIC) and residual checks. The variance explained by each selected model was obtained using the 'r.squaredGLMM' function from the *MuMIn* R Package (Bartoń, 2023). Post hoc tests for pairwise season comparisons were conducted using estimated marginal means or least squares means through the 'emmeans' function of the *emmeans* package in R (Lenth, 2023).

To examine the effects of dry-phases and environmental factors on β-diversities and their partitions, we compiled annual environmental data and explored the relationships between them as explained above (Section 2.5.1). We used the square root-transformed DD, the square root-transformed percentage of canopy, and the percentage of agriculture in the reach area to analyse the effects of these variables on all the β-diversity components. We conducted a beta regression with a log link function using the 'betareg' function of the *betareg* R package (Cribari-Neto & Zeileis, 2010). We tested betareg models using the 'lrtest' function of the *lmtest* R package (Zeileis & Hothorn, 2002) and checked the diagnostic plots to assess the residuals.

To test the effects of dry-phase duration and land use on invertebrate community composition, we used generalized linear latent variable models (GLLVMs) in the R package *gllvm* (Niku et al., 2019). Rare taxa (<0.5% abundance among all individuals and taxa with only one occurrence; Nijboer & Verdonschot, 2004) were excluded from the analysis to avoid convergence problems due to zero inflation, reducing the total number of taxa to 117. We built a GLLVM model with a zero-inflated Poisson distribution, log-link function, and one latent variable that excluded environmental predictors to generate a model-based unconstrained ordination. This approach allowed us to visually represent the similarity of the study plots based on species composition. To control for the effects of environmental factors on species, we included all possible combinations of environmental variables and time as constraining environmental predictors in the GLLVM. Due to the high computational demands of GLLVM, we limited the maximum number of predictors to three, resulting in 217 models ranked according to their second-order Akaike information criterion (AICc). We used likelihood ratio tests (LRTs) to assess the predictive ability of the two competing models, and we calculated the proportional increase (%) in deviance explained by the best environmentally constrained model. To test for trait–environment interactions, we

used fourth-corner models, where multivariate abundance data were regressed as a function of species traits and environmental predictors. Taxa traits were converted into factorial variables (Table S1.1). Specifically, we tested the interactions of the three most informative functional traits in the best environmentally constrained model, iterating all possible combinations of traits, resulting in 730 models that were ranked as explained before. We confirmed interactions between functional traits and environmental variables when the 95% confidence intervals (CIs) of each trait–environment coefficient did not overlap zero. We evaluated the significance of the whole model using LRT between nested models with or without trait interactions (Niku et al., 2019).

RESULTS

Taxonomic and functional diversity

We identified a total of 87,645 individuals belonging to 194 distinct taxa, 82 families and 146 genera (Table S1.3 and S4). Taxonomic (S) and functional (FRic) richness, as well as taxonomic diversity (H'), were highest in E10, a headwater reach located within the Natural Park (S = 44±6, H' = 2.92±0.03, and FRic = 0.49±0.06; Figure 1.2), which experienced a short dry-phase duration of 41 days during summer. These metrics were comparable to those found in A4 (S = 44±1; H' = 2.41±0.27; FRic = 0.46±0.02; Figure 1.2), a perennial reach after confluence with a high DIN concentration (Table S1.2). The EPT was highest in the headwaters (A1 = 0.45±0.05; E10 = 0.38±0.02), which showed varied levels of intermittency. Conversely, S, H', EPT and FRic were lowest in reaches with prolonged dry-phase durations (E13, E15 and A9) and downstream durations (A7, A8, and A9), with S ranging from 15±5 to 21±0, H' ranging from 1.20±0.42 to 1.48±0.42, EPT ranging from 0.20±0.08 to 0.29±0.03, and FRic ranging from 0.22±0.08 to 0.27±0.01 (Table S1.5). The functional redundancy (FRed) was greatest at the headwater sites with short drying periods, with E12 having the highest value (FRed = 0.50±0.01). In contrast, the FRed was lowest in reach E15, which exhibited the longest dry-phase duration (FRed = 0.35±0.01).

The taxonomic and functional β-diversity indices showed the highest values in reaches that completely dried in summer (E13, E14, E15 and A7) (TβD = 0.36–0.41;

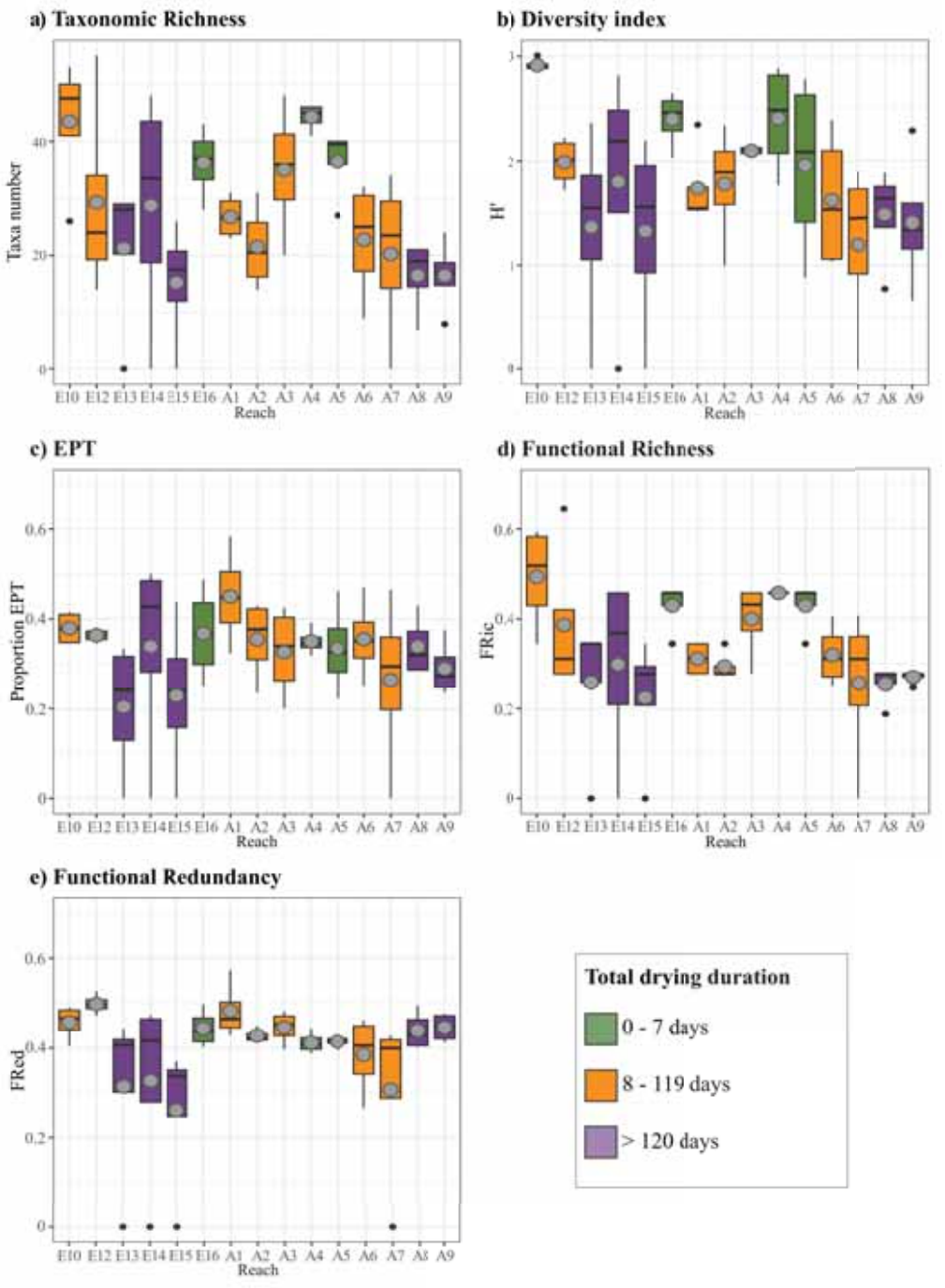


Figure 1.2. Boxplots of a) taxonomic richness, b) diversity index, c) EPT, d) functional richness, and e) functional redundancy, categorized by reach. The mean values are represented by grey dots, and the median values are represented by black lines. Points are coloured according to total dry-phase duration (days) during the study period: green, permanent (0–7 days); orange, low and medium (8–119 days); and lilac, high (> 120 days).

FβD = 0.58–0.69), followed by reaches with remnant pools, while the lowest values were observed for reach E10 (TβD = 0.19 and FβD = 0.14). Among the 15 analysed reaches, the taxonomic β-replacement component represented more than 50% of the TβD in 8 reaches, while the taxonomic β-richness difference dominated in the remaining reaches (Figure 1.3a & Table S1.6), primarily in reaches that were completely dry in summer (E13, E14, E15, and A7). However, in the functional β-partitioning, a clear dominance of the functional β-replacement component was observed, except for the reaches that were completely dry in summer (E13, E14, E15, and A7), where functional β-richness differences also dominated (Figure 1.3b & Table S1.6).

Interplay between diversity metrics and environmental factors

Taxonomic richness and the proportion of EPTs were affected only by the sampling season. Post hoc analysis revealed that the taxonomic richness was lower in the summer season than in the spring (t(41)=4.116, p value=0.001) and winter (t(41)=-4.006,

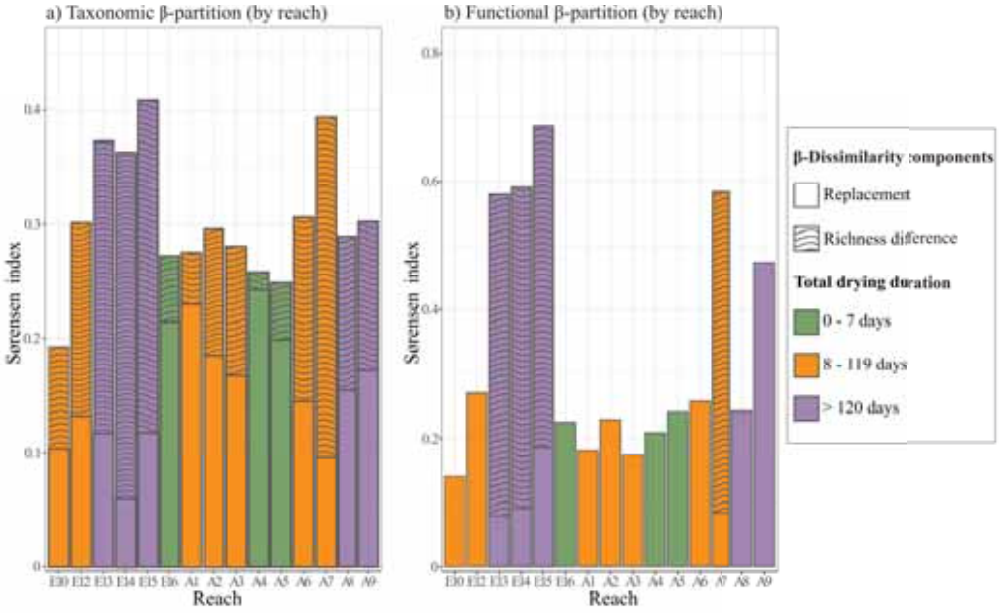


Figure 1.3. Barplots of β-diversity categorized by site, including (a) taxonomic and (b) functional aspects. The bars are divided into two β-partitioning components: solid bars represent the replacement component, while the hatched bars depict the difference in richness. The bars are coloured according to total dry-phase duration during the study period: green, permanent (0–7 days); orange, low and medium (8–119 days); and yellow, high (> 120 days).

p value=0.001). The proportion of EPTs was greater in winter than in summer (t(39)=-4.524, p value<0.001). Taxonomic diversity and functional richness were positively influenced by IHF and DIN but negatively influenced by dry-phase duration (Table 1.1). Functional redundancy was associated with conductivity, dry-phase duration, IHF, and sampling season and was found to be lowest in summer (autumn: t(39)=-3.761, p value=0.003; winter: t(39)=-4.934, p value<0.001; spring: t(39)=4.008, p value=0.002). The reach (random factor) explained variances ranging from 0.19 to 0.53 (Table 1.1).

Conversely, dry-phase duration affected both the taxonomic and functional β-diversity indices and their components (Table 1.2). DD had a positive effect, except for taxonomic β-replacement, which was negatively affected by DD. The difference in functional β-richness was too small for meaningful comparison.

GLLVM results

The environmentally constrained GLLVMs that were selected included the sampling season, DIN concentration, and dry-phase duration as drivers of invertebrate species composition, collectively explaining 75% of the total variation in the invertebrate species community composition. The ranked point estimates (±95% CIs) obtained from this model indicated a strong association between the abundance of 55% of the invertebrate species and at least one of the environmental variables, with sampling season having the greatest impact on a majority of the species (54%) (Figure S1.2). Drying, represented by DD, had a negative effect on the abundance and distribution of seven taxa (*Pisidium*, Bivalvia; *Atrichops* and sF. Clinocerinae, both Diptera; *Sialis*, Megaloptera; fam. Libellulidae, Odonata; *Chimarra* and *Holocentropus*, Trichoptera). None of the taxa were associated with the DIN water concentration (Table S1.7).

The selected model, which included traits (maximum body size, resistance form, and respiration type), both with and without interactions, did not reveal any significant trait–environment relationships and failed to explain the observed variation in the invertebrate species community composition. Additionally, the inclusion of traits accounted for a smaller proportion of the variation (4%) than did the environmentally constrained model. Only respiration type was negatively affected by all sampling seasons.

Table 1.1. Selected linear mixed models for each α-diversity index. Abbreviations: DD, total dry-phase duration; DIN, dissolved inorganic nitrogen; IHF, fluvial habitat index; canopy, percentage of canopy. Std. Error, standard error; DF, degrees of freedom. R^2 conditional, variance proportion explained by the whole model; R^2 marginal, variance proportion explained by fixed effects.

Index	Variables	Value	Std.Error	DF	p-value
S	(Intercept)	26.06	3.40	41	0.000*
	Conductivity	2.28	1.53	41	0.144
	Season.Spring	6.84	3.47	41	0.055
	Season.Summer	-7.46	3.49	41	0.038*
	Season.Winter	6.86	3.49	41	0.056
	R^2 marginal		0.17		
	R^2 conditional		0.57		
H'	(Intercept)	1.83	0.09	42	0.000*
	$\sqrt{DD}$	-0.16	0.09	42	0.03*
	$\sqrt{DIN}$	0.25	0.10	42	0.01*
	IHF	0.34	0.10	42	0.001*
	R^2 marginal		0.26		
	R^2 conditional		0.32		
EPT	(Intercept)		0.33	39	0.000*
	Conductivity		0.03	39	0.05.
	$\sqrt{DIN}$		0.03	39	0.06.
	IHF		0.03	39	0.07.
	Season.Spring		0.01	39	0.754
	Season.Summer		-0.08	39	0.022*
	Season.Winter		0.08	39	0.019*
	R^2 marginal		0.38		
	R^2 conditional		0.52		
FRic	(Intercept)	0.34	0.02	42	0.000*
	$\sqrt{DD}$	-0.03	0.01	42	0.037*
	$\sqrt{DIN}$	0.05	0.01	42	0.003*
	IHF	0.06	0.02	42	0.001*
	R^2 marginal		0.31		
	R^2 conditional		0.34		
FRed	(Intercept)	0.41	0.02	39	0.000*
	$\sqrt{DD}$	-0.03	0.01	39	0.03*
	Conductivity	0.05	0.01	39	<0.01*
	IHF	0.03	0.01	39	0.022*
	Season.Spring	0.02	0.03	39	0.582
	Season.Summer	-0.11	0.03	39	<0.01*
	Season.Winter	0.05	0.03	39	0.032*
	R^2 marginal		0.50		
	R^2 conditional		0.59		

Table 1.2. Beta regression summary tables. Abbreviations: DD, total dry-phase duration; DIN, dissolved inorganic nitrogen; IHF, fluvial habitat index; canopy, percentage of canopy. Std. Error, standard error; DF, degrees of freedom. Expl. Var., explained variance.

Index	Variables	Estimate	Std.Error	p-value
TβD	(Intercept)	-0.81	0.06	<2e-16***
	$\sqrt{DD}$	0.17	0.07	0.02*
	Agriculture	-0.06	0.07	0.42
	$\sqrt{Canopy}$	-0.10	0.07	0.16
	Phi coefficients (precision model with identity link):			
	(phi)	97.76	35.54	0.006*
	Log-likelihood: 24.89 on 5 Df		**Pseudo R^2:** 0.32	
Tβ-replacement	(Intercept)	-1.74	0.08	<2e-16***
	$\sqrt{DD}$	-0.24	0.10	0.02*
	Agriculture	-0.13	0.10	0.183
	$\sqrt{Canopy}$	-0.17	0.10	0.10.
	Phi coefficients (precision model with identity link):			
	(phi)	84.07	30.65	0.006**
	Log-likelihood: 27.69 on 5 Df		**Pseudo R^2:** 0.44	
Tβ-richness	(Intercept)	-1.75	0.15	<2e-16***
	$\sqrt{DD}$	0.53	0.18	0.003**
	Agriculture	-0.02	0.19	0.92
	$\sqrt{Canopy}$	0.02	0.18	0.93
	Phi coefficients (precision model with identity link):			
	(phi)	22.60	8.28	0.006**
	Log-likelihood: 20.1 on 5 Df		**Pseudo R^2:** 0.46	
FβD	(Intercept)	-1.16	0.10	<2e-16***
	$\sqrt{DD}$	0.27	0.12	0.031*
	Agriculture	0.01	0.13	0.94
	$\sqrt{Canopy}$	-0.12	0.13	0.33
	Phi coefficients (precision model with identity link):			
	(phi)	37.03	13.40	0.01*
	Log-likelihood: 19.17 on 5 Df		**Pseudo R^2:** 0.21	
Fβ-replacement	(Intercept)	-1.16	0.10	<2e-16***
	$\sqrt{DD}$	0.27	0.12	0.031*
	Agriculture	0.01	0.13	0.9460
	$\sqrt{Canopy}$	-0.12	0.13	0.33
	Phi coefficients (precision model with identity link):			
	(phi)	37.03	13.40	0.005*
	Log-likelihood: 19.17 on 5 Df		**Pseudo R^2:** 0.21	

DISCUSSION

In this study, we analysed the effects of drying and land use on invertebrate communities throughout a hydrological year in a Mediterranean stream network. We found that drying (represented by dry-phase duration, DD) negatively influenced the taxonomic and functional α-diversities of aquatic invertebrates. However, agricultural practices (represented by dissolved inorganic nitrogen, DIN) positively affected these diversities, partially contradicting our first hypothesis. In addition, we found that habitat heterogeneity positively influenced α-diversity, which was not initially proposed. Specifically, the negative effects of drying were less pronounced in headwater forested regions with high habitat heterogeneity than in downstream areas impacted by agricultural activities. Temporal changes in taxonomic and functional β-diversity were positively affected by drying, whereas no effect was found for any land use-related variable. This finding is partially in line with our second hypothesis. Contrary to our third hypothesis, we identified only some taxa negatively affected by drying, whereas no taxa responded to land use.

Influence of drying and land use on α-diversity in the natural intermittent network

Regarding our first hypothesis, we found a negative relationship between dry-phase duration and both taxonomic and functional α-diversity. Contrary to our expectations, agriculture (expressed as water nutrient enrichment) positively affected these diversities. Furthermore, the fluvial habitat index (IHF) had a positive impact on these variables. The negative effects of dry-phases on invertebrate communities, such as decreases in diversity, reductions in organism numbers, and shifts in functional composition and structure, are well established (Bogan et al., 2013; Lake, 2000; Leigh & Datry, 2017). Our study corroborated that drying negatively influenced taxonomic diversity, functional richness, and functional redundancy. The latter showed an increase in moderate levels of drying (less than 120 days annually; Table S1.5), but it did not counterbalance the decline in taxonomic diversity caused by prolonged dry-phase periods (Crabot, Mondy, et al., 2021). In addition, no differences were detected in the number of taxa or in the EPT, which responded to the seasonal trend and

predictable drying process, with the lowest EPT occurring during summer, the driest Mediterranean season (Bonada, Rieradevall, et al., 2007). Overall, aquatic invertebrates inhabiting the Algars stream network should be adapted to cope with both drying and seasonal patterns.

Our results suggested that the negative effects of drying were less pronounced in headwater forested reaches than in downstream areas impacted by agriculture, which may be attributed to the observed positive correlations between both α-diversities and the index of habitat heterogeneity (IHF). The IHF test assesses the relationship between habitat heterogeneity and physical variables and indicates high habitat heterogeneity and quality (Pardo, 2002). Habitat heterogeneity positively influences both taxonomic and functional diversity (Béjar et al., 2020; Milesi et al., 2016). Consequently, habitat heterogeneity can provide refuge areas for various taxa, enabling them to recolonize drying sites once the flow resumes (Dieterich & Anderson, 2000). In addition, habitat heterogeneity at drying sites can provide niches for adapted specialists, which replace taxa limited to less disturbed locations, thus decreasing diversity (Bogan et al., 2013). Furthermore, in Algars, the IHF had Spearman correlations of 0.85 with canopy cover and 0.60 with natural land cover in our study area. Headwater sites located within natural parks maintain natural riparian vegetation and are less impacted by human activities, resulting in enhanced habitat heterogeneity that supports increased invertebrate diversity (Castela et al., 2008; Urban, 2004). Hence, forested headwaters, such as those in Algars, may act as reservoirs for taxa with a range of adaptations to drying conditions (Progar & Moldenke, 2002).

Reaches with permanent flow and high agricultural influence had elevated α-diversity; conversely, intermittent reaches with high agricultural impact had the lowest α-diversity. Agricultural practices contribute to water quality deterioration and habitat destruction (Allan, 2004), but dissolved nutrients can increase the invertebrate density of some taxa (Niyogi et al., 2003), biomass (Rosemond et al., 2002), and species richness (Gruner et al., 2008) at low levels of nutrient water enrichment, as observed in the permanent reaches of Algars. However, excessive levels can depress ecosystem function or specific species components (Clapcott et al., 2012; Wang et al., 2007). Furthermore, low-flow conditions can elevate water temperature, and evaporation can escalate water salinity and specific nutrient concentrations, particularly in the form of

reduced solutes such as ammonium (Von Schiller et al., 2011). These conditions are particularly prevalent in open-canopied streams (Gómez et al., 2017), such as the downstream reaches in our study (Table S1.2). Moreover, during extended drying periods, organic matter and pollutants can accumulate and remain *in situ* until flow resumes, exposing biota to higher concentrations of contaminants, nutrients, and polluted sediments than under continuous flow conditions (Chiu et al., 2017). These factors can detrimentally impact stream invertebrate communities, especially sensitive taxa such as EPTs (Camargo & Alonso, 2006). Although we did not detect notable effects of land-use variables on EPT, our results suggested a negative impact on diversity due to the interplay between drying and agriculture.

β-Diversity driven by drying in the natural IRES network

In line with our second hypothesis, we observed that drying impacted temporal β-diversity, whereas no impact from agriculture was detected. Specifically, a positive correlation between the duration of dry phases and taxonomic β-diversity suggested alterations in the occupied trait space (Crabot, Mondi, et al., 2021). This positive relationship with dry-phase duration was also observed for the taxonomic richness difference component, indicating nestedness (Rolls et al., 2023). This effect likely results from desiccation-sensitive taxa being filtered out by drying conditions (Vander Vorste et al., 2021). For instance, individuals of *Atherix* sp. and *Hydropsyche* sp. were found at flow-connected sites in Algars during spring and summer but not at disconnected sites (Table S1.3). The negative effect of dry-phases on the taxonomic β-replacement component suggested that flow fragmentation may act as a barrier across the stream network, increasing some spatial differences. Specifically, flow fragmentation creates selective pressures on dispersers, largely due to the loss of habitat connectivity (Crabot et al., 2020). Moreover, our findings suggest that in the absence of drying, species replacement (or turnover) becomes predominant, driven by temporal shifts in community composition (Baselga, 2010; Sarremejane, England, et al., 2020).

Functional and taxonomic β-diversity, along with their associated components, showed distinct responses to drying, highlighting that functional responses supplement taxonomic information (Crabot et al., 2020). The functional β-diversity

exhibited a positive relationship with drying, which was predominantly driven by the β-replacement component. This component constituted the whole functional diversity, except in reaches that experienced complete drying during summer. Considering the selected traits, alterations in functional β-diversity also supported seasonal trait replacement, suggesting that a community of invertebrates is well adapted to the predictable seasonal drying periods typical of Mediterranean climates (Bonada, Rieradevall, et al., 2007).

Limited direct impact of drying on taxonomic composition

In addition to our third hypothesis, we did not identify any specific traits or taxa influenced by variables related to land use. However, nutrient water enrichment positively affected several diversity metrics. Conversely, we identified only a few taxa negatively affected by drying. These affected taxa were active dispersers, suggesting their ability to repopulate post disturbance and, in some instances, possibly avoid the dry phase (Bogan et al., 2017). In addition, dispersal mechanisms in small stream networks, such as those in our study area, may lead to partial community homogenization ('mass effect'), especially with flow resumption (Heino et al., 2015). Among the affected taxa, *Atrichops* sp. does not exhibit traits associated with the capacity to face the *in situ* dry phase (resistance). However, it does possess traits related to avoiding the dry phase in water, such as a short life cycle duration (≤ 1 year), or facilitating recolonization after flow resumes, such as active dispersal (resilience). Other taxa, such as *Sialis* sp. and *Pisidium* sp., exhibit resistance trait forms, such as cocoons against desiccation or diapause, respectively, but also display traits related to resilience to drying, such as active dispersal and multivoltinism, respectively (Bogan et al., 2017). Concerning dietary habits, almost all taxa affected by dry-phase duration were predators. Initially, they may benefit from drying due to prey accumulation in wet refuge areas, such as isolated pools, but are unable to cope with challenges in prolonged dry conditions (McHugh et al., 2015).

MANAGEMENT IMPLICATIONS AND FUTURE RESEARCH

Freshwater ecosystems are increasingly vulnerable to human-induced climate change. In particular, intermittent watercourses are experiencing spatial and temporal

expansion, leading to more prolonged dry events. Our study highlights the greater effect of the duration of the dry phase on invertebrate diversity than of the effects arising from different land uses within a natural intermittent stream network. Specifically, our findings suggest that both habitat heterogeneity and a certain level of agriculture in a catchment positively influence aquatic diversity. Moreover, habitat heterogeneity helps to buffer the negative effects of drying, a trend not observed at sites affected by agricultural activities. In conclusion, our research emphasizes the importance of preserving natural and forested streams. Such preservation is essential for mitigating the negative effects of drying and maintaining aquatic refuges, ensuring recolonization opportunities once flow returns across the entire stream network.

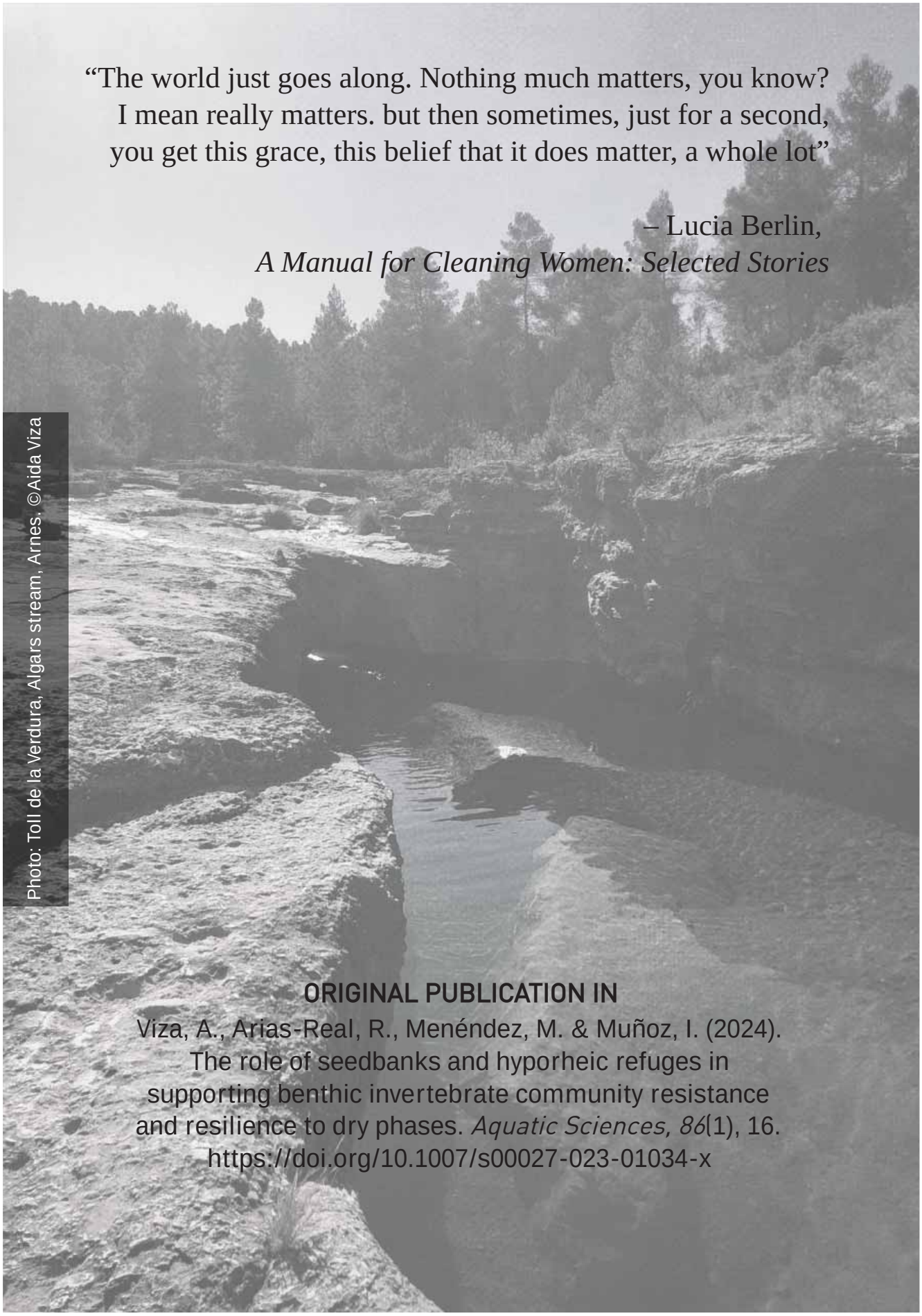
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CHAPTER 2

The role of seedbanks and hyporheic refuges in supporting benthic invertebrate community resistance and resilience to dry phases

In intermittent streams, aquatic organisms use various strategies to face with dry phases, but the relative contribution of these strategies to persist during dry phase remains unclear. Here, we investigated the *in situ* persistence of benthic invertebrates in the saturated hyporheic sediments and the 'invertebrate seedbank' that persists in dry sediments across six Mediterranean intermittent streams. Taxonomic and functional responses within hyporheic and seedbank assemblages were compared to those in the benthic assemblages under connected flow conditions by combining field and mesocosms data. The dry phase duration in each stream was calculated to assess the responses of hyporheic and seedbank assemblages. Taxonomic composition and abundance-weighted traits related to resistance and resilience to face dry phase in each assemblage type (benthic, hyporheic, seedbank) were determined. Taxonomic (richness and diversity) and functional (richness and dispersion) metrics were also calculated. We found that seedbank and hyporheic assemblages supported up to 16% and 40% of the benthic taxa, respectively. Only taxonomic and functional richness differed between assemblage types. Contrary to previous research, no clear relationship was established between diversity or the abundance of resistance traits and the duration of dry phase; however, a negative linear relationship was identified between the abundance of resilience traits and the duration of the dry phase. The increase in the frequency and duration of drying events due to climate change will reduce water availability in both saturated and unsaturated streambed sediments, compromising the persistence of aquatic biodiversity in intermittent streams.



"The world just goes along. Nothing much matters, you know?
I mean really matters. but then sometimes, just for a second,
you get this grace, this belief that it does matter, a whole lot"

– Lucia Berlin,
A Manual for Cleaning Women: Selected Stories

Photo: Toll de la Verdura, Algars stream, Arnes. ©Aida Viza

ORIGINAL PUBLICATION IN

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INTRODUCTION

Intermittent streams, characterized by shifts between wet and dry instream conditions, comprise more than 50% of global river networks (Messager et al., 2021). Flow interruption in these streams occurs gradually and varies in both time and space, modifying the lateral, longitudinal and vertical dimensions of hydrological connectivity during different hydrological phases (Datry et al., 2014). Flow contraction can culminate in the complete loss of surface water during the dry phase. The dry phase affects ecosystem functions, such as organic matter processing and sediment transport, as well as riparian and aquatic biodiversity (Larned et al., 2010). Aquatic invertebrate communities in intermittent streams have various adaptations to face dry phases, including the use of remaining wet habitats as refuges, as hyporheic zone (HZ), or the capacity to persist within dry sediment, as a 'seedbank' (Stubbington & Datry, 2013). However, the contribution of both hyporheic refuge and invertebrate seedbank, as used by benthic communities to persist during dry-phases, have not yet been compared (Hay et al., 2018; DelVecchia et al., 2022). In the context of global change, in which the spatial and temporal distribution of many intermittent streams is predicted to increase (Döll & Schmied, 2012; Sauquet et al., 2021), understanding how invertebrates persist *in situ* during dry phases in wet and dry sediments, i.e., in the hyporheic zone and invertebrate seedbank, is necessary to inform actions that preserve their biodiversity (Datry et al., 2018).

Drying alters community composition, with reductions in taxonomic and functional diversity increasing with dry-phase severity (Arias-Real et al., 2021; Crabot, Polášek, et al., 2021). In natural intermittent streams, communities are adapted to drying, displaying different combinations of functional traits that promote resistance and/or resilience to face dry phases (Nimmo et al., 2015; Bogan et al.,2015). Resilience strategies enable communities to recover after flow resumption by aquatic or aerial dispersal from refuges including upstream, downstream and/or nearby perennial reaches. Active dispersal can also enable escape of dry conditions to wet refuges, following environmental cues as flow recedes, potentially supporting subsequent community recovery (Drummond et al., 2015). In contrast, resistance strategies enable

organisms to persist *in situ* during dry phases (Bogan et al., 2017). For instance, during dry phases, some invertebrates can use isolated pools in streambeds (Bonada et al., 2006) or move to the subsurface sediments of the HZ (Stubbington, 2012; DelVecchia et al., 2022).

The capacity of the HZ to act as a refuge for aquatic invertebrates during dry phases varies spatially and temporally, influenced by factors such as sediment composition, moisture content, and water quality (Stubbington, 2012). Should the dry phase persist, water levels within the HZ may also decline, affecting taxonomic composition and leading to the loss of desiccation-sensitive taxa (Stubbington et al., 2009). After the water table recedes through the subsurface, aquatic invertebrates can only persist in damp streambed sediments as invertebrate seedbanks, which include desiccation-tolerant life stages, such as dormant eggs or juveniles (Tronstad et al., 2005). Partially desiccation-tolerant taxa can also survive within the invertebrate seedbank, provided some sediment moisture remains (Loskotová et al., 2021). The invertebrate seedbank can support over 50% of benthic taxa, and it can make a particularly substantial contribution to community recovery in certain areas, such as isolated catchments or reaches without saturated HZ (Stubbington & Datry, 2013). However, some taxa are eliminated as their taxon-specific desiccation-tolerance thresholds are surpassed (Stubbington et al., 2016). Hyporheic refuge and invertebrate seedbank are well-documented individually, but how benthic invertebrates use these different *in situ* strategies to face dry phases remains unclear.

Our aim was to characterize the relative contributions of the hyporheic refuge and the invertebrate seedbank to supporting the persistence of benthic aquatic invertebrates *in situ* during dry phases in intermittent streams, by combining field data with mesocosm experiments. We predicted that: 1) The taxonomic and functional diversity of hyporheic and seedbank assemblages will represent subsets of benthic communities, resulting in lower taxonomic and functional diversity. 2) The dry phase will result in a higher abundance of traits that confer resistance to these conditions in invertebrates from seedbank and the HZ, compared to those in benthic communities. This is because benthic taxa present in hyporheic refuge and invertebrate seedbank possess traits enabling them to tolerate dry phases. Specifically, the capacity to move into the HZ will be more abundant in taxa from HZ, whereas the ability to persist by

using any desiccation-tolerant life stage will be more abundant among taxa from invertebrate seedbank. 3) Streams experiencing prolonged dry phases will show reduced taxonomic and functional diversity in hyporheic and seedbank assemblages, and an increased abundance of resistance traits, attributed to the decline in desiccation-sensitive taxa.

MATERIALS AND METHODS

Study sites

We sampled six reaches, one in each of six intermittent Mediterranean streams across Catalonia on the northeastern Iberian Peninsula (Figure 2.1), during the summer of 2020. Selected sites had similar geology, stream order, and stream width. Specifically, stream orders spanned from three to four across an altitudinal range of 110 to 526 m.a.s.l. The geology of streams was characterized by sandstone, granite, and marl formations, with the streambeds primarily composed of gravel and coarse sand. All streams had a natural flow intermittence, experiencing dry-phase durations between 16 and 69 days, starting between early and late summer. Throughout the study period, only two reaches (Tordera and Ebro) did not dry completely as they retained pools in the streambed (personal observation). Flow resumed almost simultaneously across all streams with the onset of autumn rains in mid-September 2020, following our dry phase sample collection (Table S2.1).

Field methods

Hydrological characterization

In June 2020, before the dry phase started, a temperature data logger (HOBO® Pendant® MX2201, Onset Corp, Bourne, MA, USA) was installed in the middle of each streambed, avoiding deep pools to obtain a more representative record of the flow disconnection in the stream. Hourly temperatures were recorded until the moment of sampling collection in early September 2020. We calculated the number of days without surface water (the dry-phase duration) for each stream using the daily temperature variation between the maximum and minimum streambed temperatures. This variation indicates water presence due to the higher specific heat capacity of water

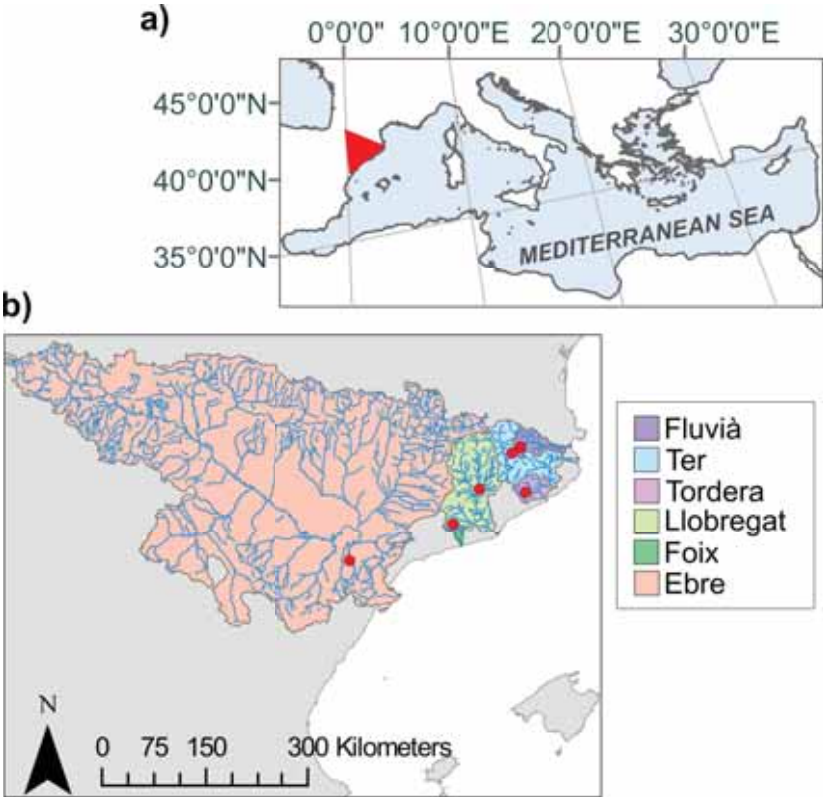


Figure 2.1. a) Location of the study area in Catalonia (NE Iberian Peninsula); b) location of the six intermittent streams, indicated by red points.

compared to air (Smith, 1975). As a result, daily variability in temperatures is lower when water is present. Air temperature and rainfall data from proximate meteorological stations were utilized to elucidate any anomalies in daily temperature fluctuations, by comparing direct measurements of air temperature and precipitation patterns with the presence of flow. However, the presence of surface water can vary within a stream reach because drying occurs more quickly in riffles than in pools (Hwan & Carlson, 2016).

Sample collection

To characterize invertebrate seedbanks, we excavated sediment samples from three points in each streambed at the end of the summer, just before the onset of autumn rainfalls, using a hand trowel. These points were selected for their lower slope, which favours the deposition of sediments. Larger surface clasts (>5 cm) were intentionally avoided, and the depth of collection was restricted to a maximum of 15 cm. Each sampled area ranged from 0.5 to 2 m^2. Approximately 8 L of dry sediment

were collected at every reach, with an attempt to collect the same quantity from each area (~ 2.5 – 3L). The sediments collected from each area were combined and transported to the laboratory.

We collected three replicate hyporheic water samples from a depth of 40 cm at 15-20 m intervals along the dry reach. Because hyporheic exchange flow can vary between riffles and pools (Käser et al., 2009), we exclusively sampled in riffle zones to minimize differences. To maximize richness estimates using a Bou-Rouch pump (Bou & Rouch, 1967), we tried to pump 20 L of hyporheic water for each replicate. However, on several occasions, we were unable to find hyporheic water and had to reposition the pump multiple times to locate it where feasible. Consequently, we were able to extract a total of 60 L of hyporheic water from only one reach, while from three other reaches, we extracted between 35 and 50 L. The HZ in two reaches, Llobregat and Fluvià, was not sampled because they were dry at the sampled depth (Table S2.1). The pumped water was filtered through a 250-µm mesh to retain invertebrates (Sánchez-Morales et al., 2018).

Benthic invertebrates were collected at each reach just after the rainy season (February) to ensure that all streams were in the flowing phase and connected. We collected five-minute kick samples with 250-µm net following a standardized multihabitat protocol that represented each habitat in proportion to its occurrence (Jáimez-Cuéllar et al., 2002).

Seedbank mesocosm setup

In the laboratory, we sieved 7.5 L of dry sediment from each reach through a 0.5-cm test sieve to remove large sediment grains. We then distributed it into three 8-L containers and covered each container with a 1-mm mesh to minimize external colonization and to retain emerging invertebrates. The containers were immediately flooded with 5 L of dechlorinated tap water, continuously aerated with air stones and maintained at room temperature under a natural photoperiod of 13:11 h (light/dark). We sampled the water column using a 250-µm hand net for 30 s at 0, 8, 16, and 32 days to collect invertebrates. After 32 days, the experiment was stopped, and all invertebrates in the sediment were collected (Datry et al., 2012), by filtering the column water and screening the sediments from each mesocosm.

Invertebrate data

All invertebrates were identified to genus except for Diptera (which were identified to the subfamily or family level), Oligochaeta (identified to the subclass level), Nematoda (identified to the phylum level), and individuals that were too small for accurate identification. Micro-crustaceans were also observed, noting only their presence or absence at the class level (Ostracoda and Copepoda) and at the genus level (Daphnia), without quantifying their abundance (Table S2.2). We aggregated all replicate samples to calculate global community diversity indices and for data analysis due to the low number of individuals per sample and the high incidence of zeros in the replicate hyporheic samples and invertebrate seedbank samples. Relative abundances, rather than absolute abundances, were calculated because different methods were used to sample each assemblage type (benthic, hyporheic, seedbank). As a result, we obtained six samples for each type of assemblage, except for hyporheic assemblages.

Resistance and resilience traits

To assess the functional aspects of each prediction, we selected and classified trait categories that promote resistance and resilience during dry phases, considering both as distinct trait classes. We considered traits associated with resistance, including any desiccation-tolerant life stages (resistance forms' trait), aerial respiration (spiracle or plastron), the capacity to move into the HZ, generalist feeding habits (herbivorous and detritivorous habits, Cummins, 1973), and small body size, as resistance trait categories. We classified female wing size, large body size, aerial active dispersal, multivoltine capacity, short life cycle duration (≤ one year), and terrestrial adult life stage as resilience trait categories (Table S2.3). Trait data were compiled from Múrria et al. (2020) and Sarremejane, Cid, et al. (2020). Values were assigned to represent the affinity of each taxon for each trait category, taking into account differences among taxa within the same genus (referred to as potential trait adaptability) using a fuzzy code approach (Chevenet et al., 1994). All category scores were standardized to proportions by setting the category sum to 1. Our final trait set had a total of 27 categories belonging to 11 traits.

For each assemblage, we calculated an abundance-weighted trait matrix by multiplying the taxa-trait matrix by the relative abundance taxa matrix (Statzner et al., 2004). Furthermore, we calculated the average abundance-weighted values for each trait class (resistance or resilience) across each assemblage type.

Taxonomic and functional metrics

To represent invertebrate seedbank 'importance' (*sensu* Stubbington & Datry, 2013), we calculated the percentage of benthic taxa present in the HZ and the invertebrate seedbank for each stream. We also identified taxa that occurred exclusively in each assemblage type. Additionally, we calculated taxonomic richness (S) and the Shannon–Wiener index (H') (Shannon, 1948) for each assemblage.

To describe functional diversity, we built a functional space (FS) using the taxa-trait matrix that included all taxa from all assemblages (72 taxa) and all trait categories. The taxa-trait matrix was used to generate a dissimilarity matrix based on the Gower distances adapted to fuzzy coding traits (Pavoine et al., 2009). The FS was created using a principal coordinates analysis conducted with the "dudi.pco" function from the R package *ade4* (Dray & Dufour, 2007). We selected the five most informative axes were based on their ability to represent the original trait-based dissimilarity among taxa (Maire et al., 2015). The 5-D FS explained 71.90% of the Gower dissimilarity matrix (with a mean squared deviation of 0.009). To identify the traits associated with each FS axis, we utilized Spearman correlation coefficients (Múrria et al., 2020). In addition, the FS was used to obtain two functional diversity metrics. The first metric, functional richness (FRic), was calculated as the minimum hypervolume of the FS occupied by invertebrate taxa in each assemblage (Villéger et al., 2008). Low values of FRic suggest that taxa capable of responding to environmental disturbance may be absent (Mason et al., 2005). The second metric, functional dispersion (FDis), represented the weighted mean distance of all invertebrate taxa to the weighted centroid of their assemblage within the FS (Laliberté & Legendre, 2010), being equivalent to the multivariate dispersion (Anderson et al., 2006). FRic and FDis are complementary metrics; FRic captures the range of the FS covered by each assemblage, whereas FDis focuses on the variation in their trait abundances (Kuebbing et al., 2018). Both metrics were calculated using the R package FD (Laliberté & Legendre, 2010; Laliberté et al., 2014).

Data analysis

To test differences between assemblage types in all metrics (taxonomic and functional metrics and the mean of abundance-weighted traits by trait class), we used the nonparametric Kruskal–Wallis test (Ostertagová et al., 2014). Additionally, post-hoc pairwise comparison tests were performed between assemblage types using a Wilcoxon rank sum test (Wilcoxon, 1945) with a Bonferroni correction to a significance level at $p < 0.05$.

To assess the effect of dry-phase duration on the resilience and resistance of aquatic invertebrates in hyporheic and seedbank assemblages, we fitted linear and non-linear regressions, utilizing nonlinear least squares for parameter estimation in the latter (Smyth, 2002). We used only data from hyporheic and seedbank assemblages, with dry-phase duration as the explanatory variable, and the mean of abundance-weighted traits for each trait class, along with their different diversity metrics, as the different response variables. The effect of dry-phase duration on individual abundance-weighted trait categories was also tested using the same approach. For linear regressions (LM), residuals were visually examined for normality and homoscedasticity. All data were analysed using R (R Core Team, 2022).

RESULTS

Taxonomic diversity

We identified a total of 24,487 individuals: belonging to 49 families and 41 genera, which included 23,970 from 34 taxa in the benthic assemblages, 415 from 24 taxa in the hyporheic assemblages, and 102 from 21 taxa in the invertebrate seedbank (Table S2.4). Four groups each accounted for more than 5% individuals of the benthic assemblages: Diptera (51.46%), Mollusca (18.19%), Oligochaeta (12.77%), and Ephemeroptera (7.43%). Three groups each accounted > 5% individuals of the hyporheic assemblages: Diptera (62.41%), Oligochaeta (22.41%), and Ephemeroptera (7.47%). Finally, five groups each accounted > 5% individuals of the seedbank assemblages: Diptera (41.18%), Oligochaeta (21.57%), Coleoptera (13.73%), Ephemeroptera (8.82%), and Hirudinea (5.88%). Diptera was the only order present in all seedbanks. Nematomorpha, Coleoptera and Ephemeroptera were present in all hyporheic assemblages.

Seedbank and hyporheic invertebrates represented 4.5–16% and 8.7–40% of benthic taxa, respectively (Table S2.5). Four taxa were exclusively found in invertebrate seedbanks (*Nebrioporus* sp., Eriopterini, Sciomyzidae, Erpobdellidae), with each taxon limited to a single stream. Similarly, four taxa were exclusive to the HZ (*Ecdyonurus* sp., Forcipomyiinae, Glossosomatidae, Polycentropodidae), each restricted to a single stream. Thirty-three taxa were present only in benthic assemblages (e.g., *Micronecta* sp. and *Sericostoma* sp.), but only the family Lymnaeidae was encountered in all benthic assemblages (Table S2.6).

Taxonomic richness was highest for benthic assemblages (S = 22±2 taxa per sample), moderate for hyporheic assemblages (11±2 taxa), and lowest for seedbank assemblages (6±1 taxa) (Kruskal-Wallis: χ^2=13.353; d.f.=2, p = 0.0013; associated Wilcoxon paired test: 0.01< all Bonferroni p-adjusted < 0.05; Figure 2.2a). The Shannon–Wiener index was comparable in all assemblages, showing values between 1.50±0.12 and 1.86±0.31 (Kruskal-Wallis: χ^2=5.5772; d.f.=2, p = 0.0615; Figure 2.2b).

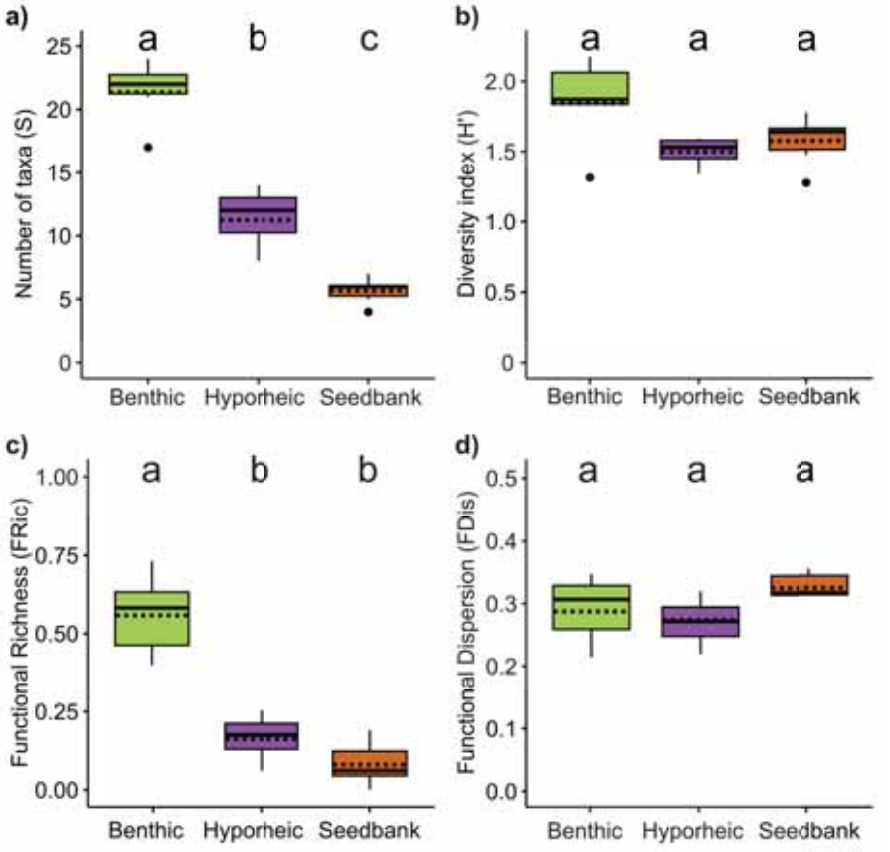


Figure 2.2. Taxonomic (a,b) and functional (c,d) metric values for benthic, hyporheic and seedbank assemblages: a) taxonomic richness (S), b) Shannon–Wiener diversity (H'), c) functional richness (FRic), and d) functional dispersion (FDis). Solid lines represent the median, while dashed lines represent the mean. Different letters indicate statistically significant differences among assemblage types.

Functional diversity

The first two axes of the FS jointly explained 43.77% of the original trait variation, with Axes 1 and 2 explaining 23.79% and 19.98%, respectively (Figure 2.3a). Axis 1 was highly correlated (>0.50, Spearman correlation) with feeding habit, body size, voltinism and female wing length, aligning with the resistance trait categories at one extreme (generalist feeding habits and small body size) and the resilience trait categories at the other (large body size and high female wing length). Axis 2 was highly correlated (>0.50, Spearman correlation) with adult life stage, life cycle duration, and female wing length, primarily corresponding to the resilience trait categories at one of its extremes (terrestrial adult stage and a life cycle duration of one year or less; Table S2.8). Orders plotted in three main clusters: Diptera, Ephemeroptera, Plecoptera and Trichoptera in

the upper left-hand quadrant; Odonata and Megaloptera with positive Axis 1 values; and all eight other orders with negative Axis 2 values (Figure 2.3a).

Benthic assemblages occupied more functional space than their respective hyporheic and seedbank assemblages (Figure 2.3b). Two hyporheic assemblages occupied > 50% of the total FS, while the other two hyporheic assemblages occupied less space. All seedbank assemblages occupied < 50% of the FS, and the two smallest FS corresponded to the streams without HZ (Figure 2.3b). Functional richness was highest for benthic assemblages (0.58±0.11), and lowest for hyporheic (0.06±0.01) and seedbank (0.05±0.01) assemblages (Kruskal-Wallis: χ^2=11.765; d.f.=2, p = 0.0028; associated Wilcoxon paired test: Bonferroni p-adjusted$_{\text{all benthic}}$ = 0.014; Figure 2.2c). Functional dispersion was not significantly different among assemblage types, showing values between 0.27±0.05 and 0.32±0.03 (Kruskal-Wallis: χ^2=4.0772; d.f.=2, p = 0.1302; Figure 2.2d).

Resistance and resilience traits

The mean of abundance-weighted resistance trait categories was lowest for hyporheic assemblages (0.25±0.20), and highest for benthic assemblages (0.47±0.05) and seedbank assemblages (0.35±0.11) (Kruskal-Wallis: χ^2=11.486; d.f.=2, p = 0.0032; associated Wilcoxon paired test: Bonferroni p-adjusted$_{\text{all hyporheic}}$= 0.015; Figure 2.4a). Generalist feeding habits were the predominant resistance trait category across all assemblage types, with weighted abundances ranging from 0.51±0.14 to 0.82±0.13. This was closely followed by the small body size, with weighted abundances between 0.35±0.31 and 0.58±0.17. The capacity to move into the HZ demonstrated moderate weighted abundances in both benthic (0.28±0.05) and hyporheic (0.19±0.06) assemblages, whereas the abundance of a resistance forms' trait was more pronounced in dry sediment (0.47±0.15) (Table S2.9). Two trait categories varied among the assemblage types: resistance forms' trait, which was lowest for HZ (Kruskal-Wallis: χ^2=9.7996; d.f.=2, p = 0.0074; associated Wilcoxon paired test: 0.02<Bonferroni p-adjusted$_{\text{hyporheic}}$< 0.04), and aerial respiration, which was highest for the seedbank (Kruskal-Wallis: χ^2=13.066; d.f.=2, p = 0.0015; associated Wilcoxon paired test: 0.006<Bonferroni p-adjusted$_{\text{all seedbank}}$< 0.02).

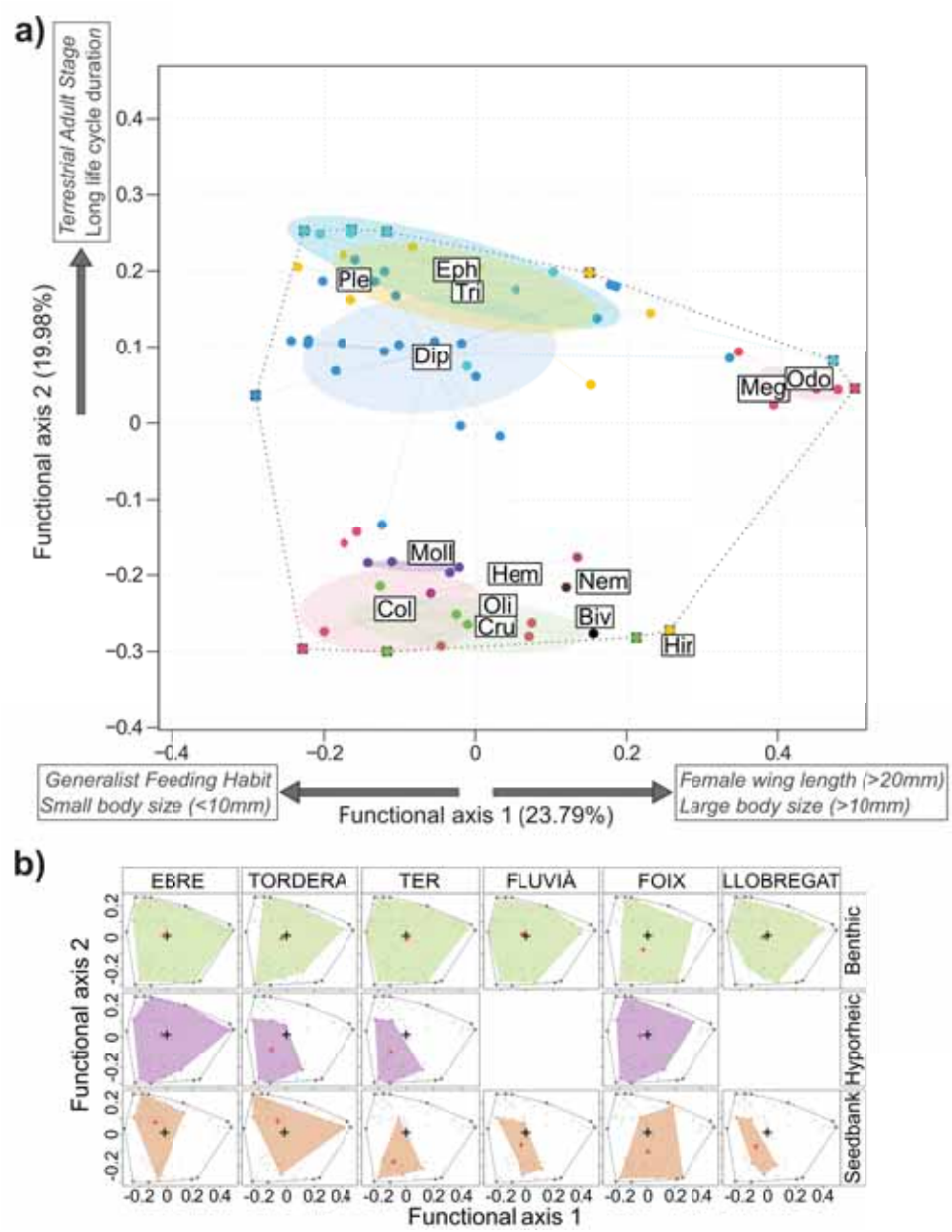


Figure 2.3. Functional space (FS) plot on two axes: a) FS with taxa represented by points coloured according to taxonomic group. The dotted line denotes the boundary of the total FS created by all taxa. Categories of selected traits that are correlated with each axis are located at the corresponding axis extreme. b) FS occupied by each assemblage, with small points representing individual taxa; red crosses indicating the assemblage centroids; and black crosses marking the centroid of the all-taxa ordination. Abbrev.: Biv.: Bivalvia; Col.: Coleoptera; Cru.: Crustacea; Dip.: Diptera; Eph.: Ephemeroptera; Hem.: Hemiptera; Hir.: Hirudinea; Meg.: Megaloptera; Moll.: Mollusca; Nem.: Nematomorpha; Oli.: Oligochaeta; Odo.: Odonata Ple.: Plecoptera; Tri.: Trichoptera.

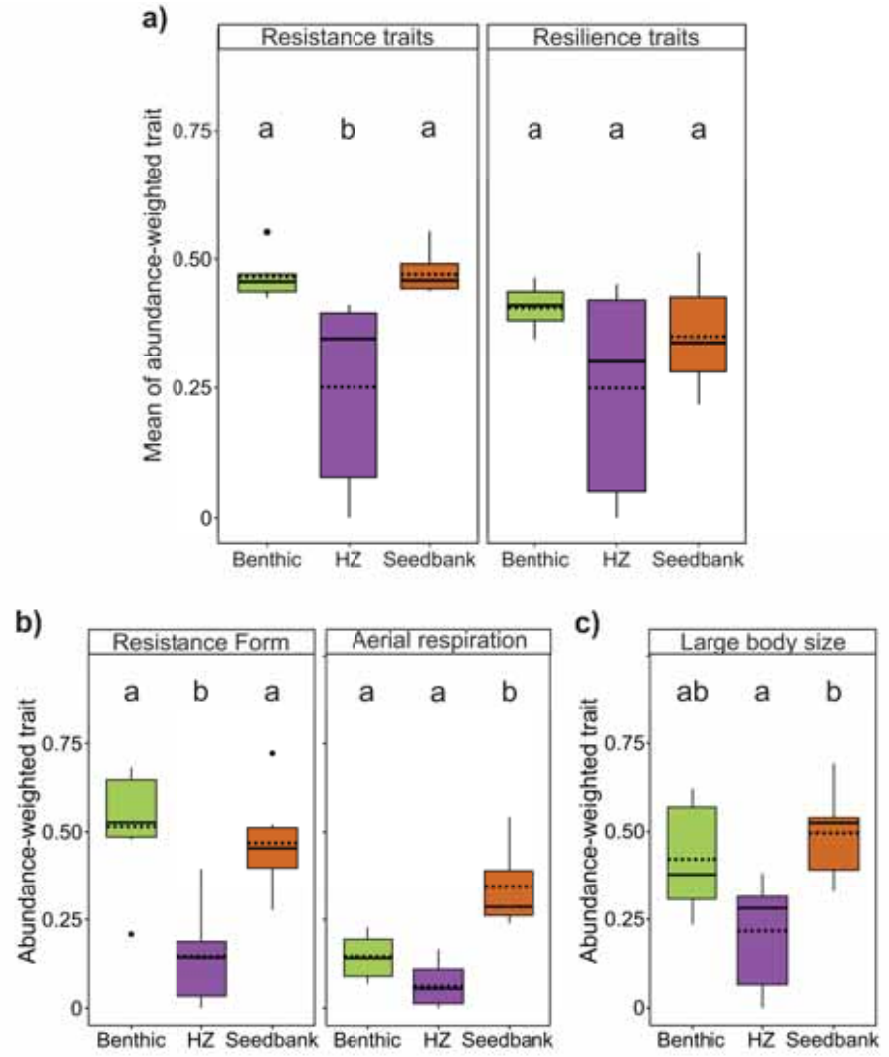


Figure 2.4. Abundance-weighted traits for benthic, hyporheic and seedbank assemblages: a) mean of abundance-weighted trait by trait class; b) resistance categories, and c) resilience category. Solid lines indicate the median, and dashed lines represent the mean. Traits and trait categories are described in Table S2. Different letters indicate statistically significant differences.

The mean of abundance-weighted resilience trait categories was statistically comparable in all assemblages, showing values between 0.25±0.21 and 0.41±0.04 (Kruskal-Wallis: χ^2=1.8382; d.f.=2, p = 0.3989; Figure 2.4a). A short life cycle duration (≤ one year) was the predominant resilience trait category for all assemblage types, with weighted abundances ranging from 0.45±0.40.01 to 0.72±0.11. In benthic and hyporheic assemblages, this was followed by the terrestrial adult stage (0.65±0.20 and 0.40±0.38, respectively) and multivoltinism (0.47±0.13 and 0.32±0.28, respectively). In

contrast, in seedbank assemblages, the large body size and terrestrial adult stage were the subsequent most abundant trait categories (0.50±0.14 and 0.42±0.30, respectively). Notably, large body size varied among the assemblage types (Kruskal-Wallis: χ^2=6.8843; d.f.=2, p = 0.032; associated Wilcoxon paired test: Bonferroni p-adjusted$_{seedbank\text{-}hyporheic}$=0.039; Figure 2.4c).

Effects of dry-phase duration on taxonomic and functional assemblages

Only the mean of abundance-weighted resilience traits differed in response to dry-phase duration in hyporheic and seedbank assemblages following a linear regression (LM: $F_{1,8}$=17.75; d.f.=8, p=0.0029). Notably, as the dry-phase duration increased, the abundance of these traits decreased (Figure 2.5a). Specifically, both the terrestrial adult stage (LM: $F_{1,8}$=34.9; d.f.=8, p=0.0003) and short life cycle duration (LM: $F_{1,8}$=14.51; d.f.=8, p=0.0052) also followed a negative linear relationship with the dry-phase

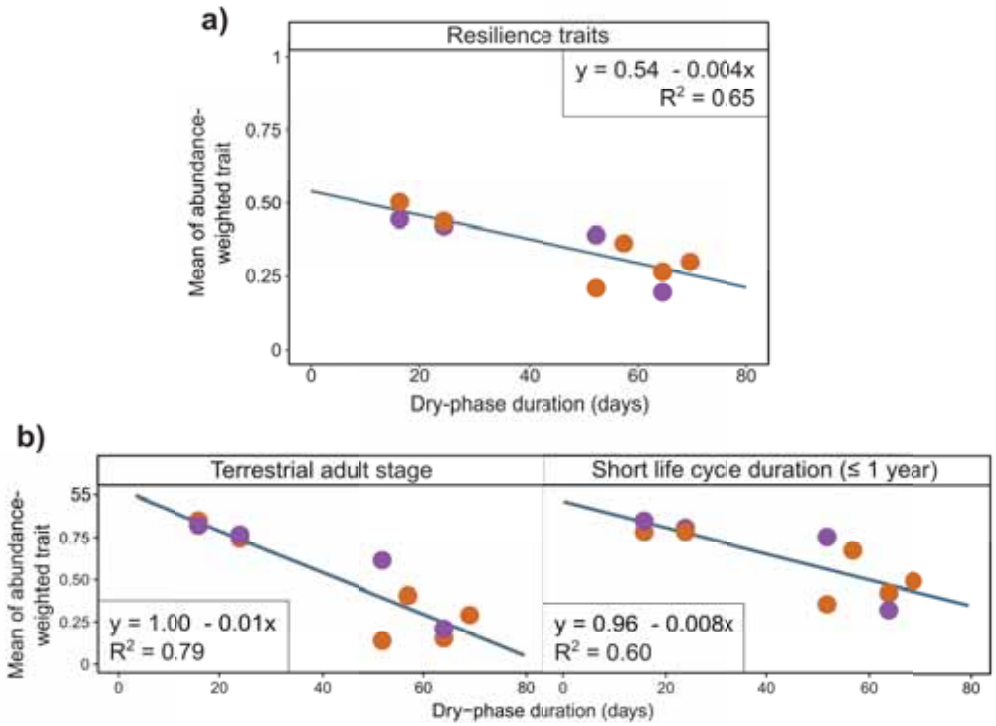


Figure 2.5. Linear relationship between dry-phase duration and a) the mean of abundance-weighted resilience traits and b) the terrestrial adult stage and short life cycle duration, both categories of resilience traits. Lilac points represent hyporheic assemblages, whereas orange points represent seedbank assemblages. Benthic assemblages were excluded.

duration (Figure 2.5b). However, taxonomic and functional metrics, along with the mean of abundance-weighted resistance traits, did not conform to any discernible model (Figure S2.1).

DISCUSSION

This study is the first to compare the contribution of seedbank and hyporheic refuge used by benthic aquatic invertebrates to face dry phases *in situ* in intermittent streams. Our results showed that persistence in the seedbank and the HZ are strategies employed by a subset of benthic invertebrate taxa during dry phases in Mediterranean streams. Taxonomic and functional richness were higher in benthic assemblages than in those in the HZ and in invertebrate seedbanks, confirming our initial hypothesis that both hyporheic and seedbank assemblages are subsets of benthic assemblages. Contrary to our second hypothesis, no significant differences in the abundance-weighted resistance traits were observed between benthic and seedbank assemblages; consistently, hyporheic assemblages showed the lowest abundances. Finally, while no clear relationship was established between diversity or the abundance of resistance traits, and the duration of dry phases, as was expected, a linear negative relationship was identified between the abundance of resilience traits and the duration of the dry phase.

Contribution of hyporheic and seedbank invertebrate assemblages supporting benthic communities

Consistent with our first hypothesis, nearly all taxa and traits observed in the HZ and invertebrate seedbanks were also identified in benthic communities, which showed the highest taxonomic and functional richness. These findings suggest that hyporheic and seedbank assemblages represent subsets of the benthic communities (Stubbington, 2012; Stubbington & Datry, 2013). The taxonomic overlap among all assemblage types, ranging between 5 and 40%, demonstrated that some benthic taxa might persist in the HZ and/or the seedbank. Concretely, the percentage of benthic taxa in the HZ (8.7–40%) corresponded to some previous studies. For instance, Boulton (1992) found that the 35% and the 69% of benthic taxa were present in the HZ of a temperate and arid intermittent streams,

respectively. However, the taxonomic richness in these sites was limited to 8 and 10 taxa, figures that are similar to the taxonomic richness found in the HZ of our study (between 8 and 13 taxa). In contrast, Datry (2012) reported a 75% overlap of benthic taxa in HZ in a temperate stream but noted a 10% decrease in similarity between benthic and hyporheic assemblages for every 10 days of prolonged dry-phase duration. On the other hand, the percentage of benthic taxa found in the invertebrate seedbanks in our study streams (between 4.5% and 16%) was lower than in previous studies. For example, Datry et al. (2012) found two to three times more benthic taxa in the invertebrate seedbank of a temperate intermittent stream under similar dry-phase durations. However, these percentages varied from 33 to 5%, in arid and Mediterranean streams, respectively, with low taxonomic richness (9 and 3, respectively), similar to our findings (Stanley et al., 1994; Chester & Robson 2011).

Oligochaeta and Diptera were abundant in the studies previously mentioned (Boulton, 1992; Chester & Robson, 2011; Datry, 2012; Datry et al., 2012). In our streams, both Oligochaeta and multiple Diptera families were also well-represented in all assemblage types. Both groups include taxa with desiccation-tolerant life stages and the capacity to move into the HZ, with certain Oligochaeta species also having aerial respiration (Tachet et al., 2010). Moreover, these groups include semiaquatic species, explaining their potential to be among the few taxa that persist in invertebrate seedbanks during extended dry phases (Tronstad et al., 2005; Chester & Robson, 2011; Datry et al., 2012; Stubbington et al. 2016). Some Ephemeroptera found in the HZ, like *Caenis* sp., are characterized as a burrower and can actively move into the HZ (Tachet et al. 2010; Robertson, 2010). However, the early instars of *Ecdyonurus* sp., and *Baetis* sp., are transported passively into the HZ by downwelling water, resulting in their temporary inhabitation of these subsurface sediments (Boulton, 2000; Tachet et al. 2010). On the other hand, Ephemeroptera found in seedbanks, including *Procloeon* sp. and *Caenis* sp., have summer egg diapause (Clifford 1982; Brittain 1990). Coleoptera taxa identified in the HZ can move into this refuge, whereas none of those recorded in the seedbank (e.g., *Nebrioporus* sp.) are recognized as having desiccation-tolerant life stages (Tachet et al. 2010). The survival of these Coleoptera in the dry streambed can be attributed to their aerial respiration and certain level of desiccation tolerance, conferred by their impermeable protective cuticle (Holdgate, 1956; Pallarés et al.,2017).

We identified seven benthic taxa in the HZ that were not present in the invertebrate seedbanks, such as *Hydropsyche* sp., which does not show desiccation-tolerant life stages (Tachet et al., 2010). Conversely, six benthic taxa were found in the invertebrate seedbanks but not in the HZ, such as *Procloeon* sp., which enters summer diapause and is multivoltine, adaptations for avoiding aquatic environments during the dry phase (Bonada, Rieradevall, et al. 2007). Furthermore, four taxa exclusively in the HZ, with three represented by 1–2 individuals, and *Ecdyonurus* sp. by 10 individuals in a single sample. Conversely, four taxa were only found in the invertebrate seedbank, each represented by 4-6 individuals per sample. Given the very low densities of these taxa in both the HZ and in invertebrate seedbanks, we suggest that they may also have been present in the benthic sediments but were missed by kick sampling. This method captures only a proportion of the taxa present (e.g. 62% and 78% of families and 50% and 68% of species in three and six minutes sampling, respectively; Furse et al., 1981).

Differences in trait responses across assemblage types

Contrary to our second prediction, the hyporheic assemblages showed the lowest abundance-weighted resistance traits, in part because small body size, generalist feeding habits, and the capacity to move into the HZ were common resistance traits in benthic and seedbank, as well as hyporheic assemblages. These traits are either directly or indirectly associated with the ability to move into and persist within the HZ. For instance, body size affects an organism's ability to penetrate sediment due to the dimensions of interstitial pathways (Stubbington, 2012), while generalist feeding habits are advantageous given the limited abundance and diversity of food resources in the HZ (Burrell & Ledger, 2003). In addition, a few hyporheic taxa (e.g., Glossostomidae and Forcipomyinae), although not burrowers, show crawler behaviour and small sizes, enabling them to seek refuge in the HZ following the water table recedes through the subsurface sediments in dry phases (Vander Vorste et al., 2016; Maazouzi et al., 2017). This ability is influenced by interactions between taxon characteristics (i.e., their traits) and environmental factors, including sediment characteristics, such as grain size, and local hydrological conditions, such as the direction and strength of hyporheic exchange (Stubbington, 2012; Dole-Olivier et al., 2022).

Seedbank and benthic assemblages had similar abundances of resistance traits, with the third most abundant trait in seedbank assemblages being the presence of resistance forms' trait. In contrast, aerial respiration showed low weighted abundances (<0.4) across all assemblages, and had its highest abundance in seedbank assemblages. Although aerial respiration becomes particularly advantageous when water flow decreases and water quality deteriorates, especially when dissolved oxygen concentrations decline (Bonada, Rieradevall et al., 2007; Mellado-Díaz et al., 2007), it is not necessarily associated with the persistence in HZ or in invertebrate seedbanks, even though if some taxa have both trait classes. For instance, within the Mollusca, most freshwater pulmonates can tolerate hypoxic conditions, as may occur in the HZ during dry phases, and also tolerate exposure to air. They can also extend this tolerance by entering a dormant, aestivating state (Poznańska et al., 2015).

On the other hand, we did not find differences in abundance-weighted resilience traits between assemblage types. The only exception was the large body size trait category, which showed the lowest abundances in hyporheic assemblages, suggesting that maximum body size may limit the use of HZ (Mathers et al., 2019). The similar trait composition across assemblage types and the taxonomic and functional overlapping (see above), reflect the dominance of traits that enable aquatic invertebrates to tolerate dry phases in intermittent natural streams of Mediterranean basin (Bonada, Dolédec, et al., 2007).

Dry-phase duration and resistance strategies

Contrary to our third hypothesis, taxonomic and functional diversity, as well as resistance traits, did not show a clear relationship with the duration of dry phase in hyporheic refuges and seedbanks. Despite the limited number of samples and total individuals, we identified a negative correlation between abundance-weighted resilience traits and the duration of dry phase. As dry-phase duration increases, environmental conditions become harsher, filtering out the less desiccation-tolerant taxa (Datry, 2012; Datry et al., 2012), which may also possess resilience traits. In addition, we found that the resilience trait categories of terrestrial adult stage and short life cycle duration (≤ one year) also showed a negative linear relationship with dry phase duration. The decline of these traits may indicate avoidance behaviour in

response to harsher conditions during more severe dry phases (Strachan et al., 2015). However, we must be cautious with these relationships given the low number of samples, which prevents drawing definitive conclusions.

On the other hand, two of the study reaches with the longest dry phases (Llobregat and Fluvià) lacked water in the HZ, preventing invertebrates from finding refuge in the shallow hyporheic sediments that we sampled, or forcing invertebrate to migrate into deeper sediments find refuge (Clinton et al., 1996). The effectiveness of most resistance strategies decreases with an increase in dry-phase harshness, influenced by the presence of water in the HZ or isolated pools, or moisture in the streambed sediment (Bogan et al., 2017). With extended dry phases and water loss, only few invertebrates are adapted to such harsh conditions (Fritz & Dodds, 2004). For instance, many invertebrate seedbank taxa, which have various desiccation-tolerant life stages (e.g., eggs, juveniles), can persist during moderate-intensity dry phases, but as intensity increases, only taxa with cocoons and housing against desiccation can survive (Crabot, Mondy et al. 2021). Consequently, extended, severe dry phases can significantly alter aquatic invertebrate community composition (Doretto et al., 2018; Chanut et al., 2022).

CONCLUSIONS AND PROSPECTS FOR FUTURE RESEARCH

Future research is required to extend our understanding of the invertebrate traits associated with resistance and to evaluate the impact of dry phases on the effectiveness of resistance strategies (Stubbington & Datry, 2013; DelVecchia et al., 2022). Our results showed that the taxa within hyporheic refuges and invertebrate seedbanks constituted up to 40% and 16%, respectively, of benthic invertebrate taxa. Additionally, a similar abundance of traits to face with the dry phase was observed across all assemblage types, suggesting a biota adapted to seasonal drying events in Mediterranean streams. Ongoing climate change, as well as human activities including water abstraction, are intensifying the frequency and duration of stream drying (Datry et al., 2018). This escalation may compromise the availability of water necessary to sustain the HZ and to maintain adequate moisture levels to support life in streambed sediments. In light of these challenges, freshwater management strategies should aim to ensure a sufficient

supply of water to preserve aquatic biodiversity and the integrity of their recovery mechanisms during dry phases in naturally intermittent streams.

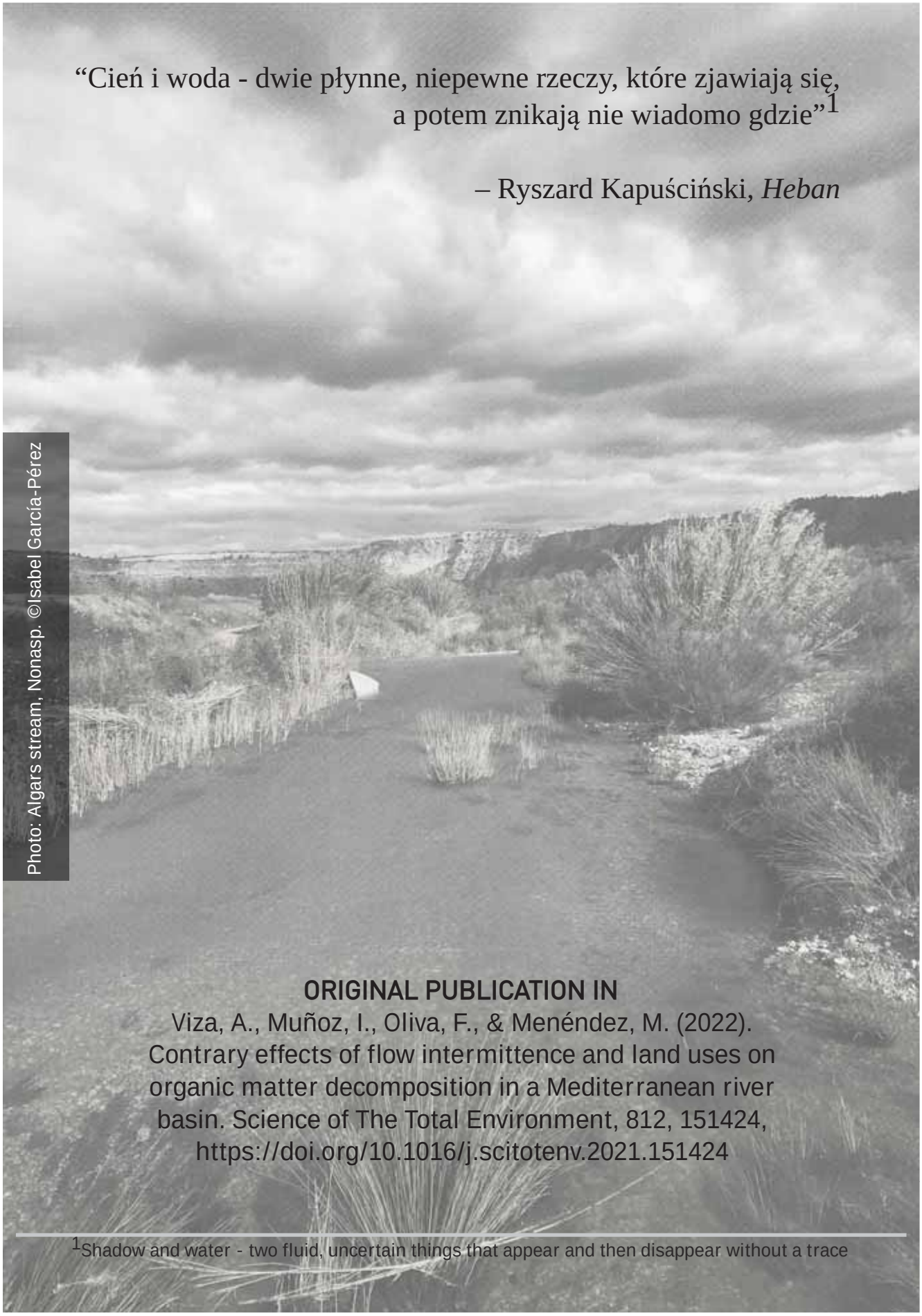
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CHAPTER 3

Contrary effects of flow intermittence and land uses on organic matter decomposition in a Mediterranean river basin

Flow interruption in intermittent rivers (IRs) generates a mosaic of terrestrial and aquatic habitats across the river network affecting ecosystem processes, as organic matter (OM) decomposition. Water use for farming in arid and semi-arid climates intensifies the dry conditions and affect local river characteristics. In that way, flow intermittence and the distribution of land uses may affect the OM processing along the river. To understand the role of IRs in global OM dynamics and how global change affecting water flow regimes determines these dynamics, it is important to estimate OM-processing rates at a basin scale. The aim of this study was to evaluate the effect of the intensity of flow intermittence on OM processing, and how this effect was modulated by local environmental factors related to land uses across a Mediterranean river basin. To do this, wood decomposition (mass loss and fungal biomass) was selected as a functional indicator. Drying duration and frequency were measured to characterize flow intermittence in different reaches along the river, as well as local environmental factors. Linear models stablished the role of factors on decomposition. The results showed that differences in decomposition rates across the river network were negatively related to the duration of flow interruption. Dissolved inorganic nitrogen associated with agriculture counteracted the negative effect of intermittence on mass loss (increasing by up to three times); but with a higher duration of dry conditions, its effect was insignificant. An increase of 20% of canopy (higher in natural areas) resulted in increases of up to 5% of mass loss. Overall, our study is relevant to understanding the interaction between flow intermittence and land uses on OM processing, especially considering the intensification of flow intermittence and its increased distribution to other regions, which is expected to be a consequence of climate warming and human activities.



"Cień i woda - dwie płynne, niepewne rzeczy, które zjawiają się, a potem znikają nie wiadomo gdzie"[1]

– Ryszard Kapuściński, *Heban*

Photo: Algars stream, Nonasp. ©Isabel García-Pérez

ORIGINAL PUBLICATION IN

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[1]Shadow and water - two fluid, uncertain things that appear and then disappear without a trace

INTRODUCTION

Intermittent rivers (IRs) are characterized by periods of flow cessation and are distributed across the world. Flow intermittence in IRs can be natural and/or induced by human impacts, such as water extraction, flow regulation, changes in land use, or climate change (Steward et al., 2012). Flow cessation implies the disruption of hydrological connectivity in one or more spatial dimensions (longitudinal, lateral and/or vertical) under the hierarchy of the time dimension that can reduce or extend the duration of flow cessation (Ward et al., 1989; Boulton et al., 2017). At the river basin scale, this variability results in a mosaic of terrestrial and aquatic habitats constantly shifting as a consequence of flow contraction and resumption (Datry et al., 2014) and contributes differentially to the processing of organic matter (OM). As the duration of the dry conditions and rewetting periods is a key factor in controlling microbial activity and OM decomposition (Foulquier et al., 2015), this spatial organization of habitats across the basin jointly with the intensity of temporality will determine the annual OM budget in IR networks, which represent more than half of global river networks (Messager et al., 2021). To obtain insights into the role of IRs in global OM dynamics and how climate change and other factors affecting flow regimes determine these dynamics, it is important to estimate differences in OM-processing rates across the basin in IRs, including different habitats and conditions.

An increase in agricultural practice intensification in recent decades has generated large impacts on freshwater ecosystems, such as water nutrient enrichment, especially inorganic N and P concentrations (Paul et al., 2006). In addition, agriculture is the economic sector with the highest water demand, and 40.4% of the total water use in Europe in 2015 was for cultivation practices (EEA, 2018). In water-limited areas, such as in the Mediterranean region, the farming of crops has changed from rainfed to irrigated agriculture with higher water consumption. As a consequence, in Mediterranean regions, where IRs are the most common fluvial ecosystems due to their natural flow regimes, freshwater demand has increased mainly in summer when the water flow is the lowest (García-Ruiz et al., 2011), intensifying dry conditions and flow disconnection in the basin. Land for agricultural uses also modifies stream

geomorphology, riparian canopy and hydrochemistry (e.g., higher nutrient concentration and presence of pollutants), and consequently, resulting effects are expected on community diversity and ecosystem functioning (Cooper et al., 2013). Knowledge about how these effects interact with flow intermittence is still limited mainly at basin scale where these pressures change spatially.

OM decomposition is a key process in stream ecosystems and represents an important source of carbon and energy for stream food webs (Tank et al., 2010); therefore, it has been suggested as an indicator of ecosystem functioning (Young et al., 2008). OM decomposition is a result of the interaction between several abiotic and biotic factors. The main biological drivers of stream OM decomposition are microbial decomposers (fungi and bacteria) and invertebrate shredders. In the first stages, aquatic hyphomycetes are the first colonizers producing detritus rich in nutrients and transforming leaf litter into a more palatable resource for shredders (Bärlocher, 1992; Gessner et al., 2010). The decomposition process is also affected by environmental factors, such as temperature (Geraldes et al., 2012), dissolved nutrients (Menéndez et al., 2011), pH (Kok and Van der Velde, 1994) or flow regimes (Martínez et al., 2015). For instance, increased inorganic N and P concentrations stimulate the activity of aquatic hyphomycetes (Sridhar and Bärlocher, 2000; Menéndez et al., 2011), particularly for low-quality substrates (i.e., low nutrients and high lignin content) (Ferreira et al., 2006). In addition, the duration of flow interruption affects fungal activity as a result of the transition between aquatic and terrestrial habitats but fungal activity recovers when flow resumes (Mora-Gómez et al., 2018). Traditionally, OM decomposition was measured using the mass loss of leaf litter bags, which can be variable depending on litter quality because it has a high variability in chemical composition (Lecerf and Chauvet, 2008). Nevertheless, several authors have proposed using alternative standardized substrates, which are less variable in their chemical composition (Tiegs et al., 2007; Young et al., 2008). One of these proposals is wooden sticks (Díez et al., 2002). Although wood decomposition is considered a slow process due to its recalcitrant nature, wooden sticks are small pieces with a high surface-to-volume ratio, which favours their decomposition (Arroita et al., 2012). In addition, wood decomposition responds in the same way to environmental factors as leaf decomposition (Gulis et al., 2004).

Studies at the basin scale have important implications for ecosystem services and functioning and, especially, for water resource management (Allan and Johnson, 1997; Elosegi and Sabater, 2013). Previous studies have shown that at this scale, the variability of OM decomposition depends especially on local factors, such as hydromorphological alterations (e.g., flow regulation) (Abril et al., 2015), land uses (Paul et al., 2006; Tonin et al., 2018) or dissolved nutrients (Molinero et al., 1996). For instance, Paul et al. (2006) analysed the effect of different catchment land uses on leaf decomposition and found that agricultural and urban land uses enhance leaf litter decomposition as a consequence of water nutrient enrichment, especially phosphorous. In the same way, Abril et al. (2015), identified a unimodal distribution of decay rates related to total agricultural land use. Aristi et al. (2012) also found a hump-shaped relationship between decomposition rates and phosphorous related to human activities in permanent reaches of four Mediterranean basins on the Iberian Peninsula. However, there is little knowledge about what happens at the basin scale in IRs considering spatial and temporal variations in flow, especially in understanding the interactions between natural flow intermittence and human stressors, such as nutrient addition (Von Schiller et al., 2017).

The aim of this study is to evaluate the effect of the intensity of flow intermittence during a hydrological year on OM decomposition and how it is modulated by land uses at a river basin scale. To accomplish this objective, the decomposition rates and fungal biomass of wood sticks incubated in 16 sites along a small Mediterranean river are analysed in relation to flow intermittence descriptors and local environmental parameters. Part of the studied basin is located in a protected area conserving the natural vegetation; the other part is characterized by land used for agriculture, whereas urban uses were incidental. We hypothesize that a higher intensity (duration and frequency) of intermittence will negatively affect OM decomposition rates and fungal biomass. However, as agricultural activities can increase water nutrient availability to the microbial community, enhancing its activity and biomass accrual, the negative effects of flow intermittence will be reduced in those reaches where the effect of agriculture is present. This study examines at river basin scale, the spatial variation in the quantity of OM processed and relate it to differences in flow patterns (from permanent reaches to ephemeral) and land uses (agricultural and natural uses).

MATERIALS AND METHODS

Study area

This study was conducted in the catchment of the Algars River, which flows into the Matarranya River, a tributary of the Ebro River, located in the northeastern part of the Iberian Peninsula (Figure 3.1). The total area of the catchment is 405 km^2, and the mainstream is 70 km in length. Algars headwaters are divided into two streams, Estrets and Algars, located in the natural park of Els Ports. The climate is typically Mediterranean characterized by scarce precipitation concentrated in spring and autumn with drier and warmer summers. The main land uses were extensive agriculture (44.6% of the total basin, mainly olive groves, fruit trees and vineyards), and natural vegetation (55.3%, mainly coniferous forests, bare rocks, sclerophyllous vegetation and transitional woodland-shrub) while urban land uses were incidental (<0.45%) (Corine Land Cover, 2018). We selected 16 sites across the catchment, 7 sites on the Estrets stream, 3 sites on the Algars headwater stream before the confluence with the Estrets and 6 sites on the Algars mainstream after the confluence (Figure 3.1). The study was conducted during a hydrological year (November 2018 to November 2019). During this period, the accumulated precipitation in the basin was 368.9 mm, and the mean temperature was 15.1°C, with a maximum temperature of 40.6°C at the end of June and a minimum temperature of -4 °C in January (Meteorological Service of Catalonia, METEOCAT).

Stream flow intermittence

To characterize flow intermittence, two variables were calculated. The total non-flow days, as a measure of the duration of intermittence, and the total times that flow was interrupted, as a measure of the frequency of intermittence. Both were calculated at each site using the water level and daily streambed temperature variation as an indicator of water presence, recorded every hour during the year with leveloggers (Solinst Levelogger Edge, full-scale reading accuracy of 0.05%) placed on the streambed (Constantz et al., 2001). To correct the recorded data, atmospheric pressure variations from barologgers (Solinst Barologger, full-scale reading accuracy of 0.05%) installed at the riparian zone at each site were used.

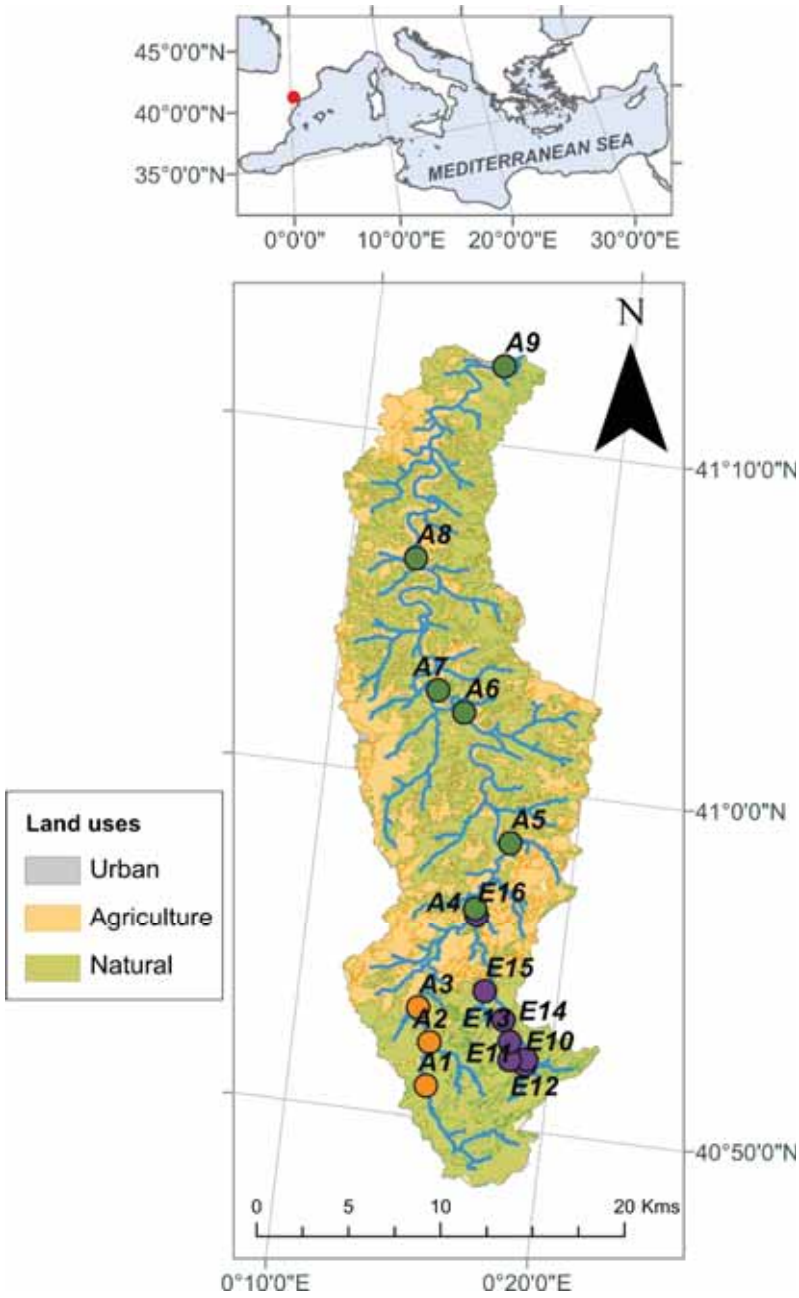


Figure 3.1. Location of Algars basin (NE Iberian Peninsula) in the Mediterranean region and land uses distribution in the river basin. Natural land-uses are in green, agricultural land-uses are in orange and urban land-uses in grey. Dots indicate the location of study sites. Purple dots correspond to Estrets stream sites, orange dots correspond to Algars stream sites before the confluence, and green dots correspond to sites on the Algars stream after the confluence.

Environmental parameters

During the study period, water physical and chemical parameters were seasonally (November 2018, February 2019, May 2019 and August 2019) measured at each site (Table 3.1 & Table S3.1). A portable probe (YSI Professional Plus Multiparameter Instrument, USA) was used *in situ* for electric conductivity, water temperature, water dissolved oxygen and pH (±1 µs cm^{-1}, ± 0.1°C, ± 0.1 mg L^{-1} and ± 0.005 pH, respectively). To characterize water nutrient concentrations, three water samples were filtered through glass fibre filters (0.7-µm pore size; Whatman GF/F, Germany) into prewashed polyethylene containers, transported to the laboratory and stored at 4°C in the dark until analysis. Water samples were analysed by ionic chromatography (± 2.8% at 1 ppm; IC5000, DIONEX, USA) to obtain concentrations of magnesium (Mg^{+2}), calcium (Ca^{+2}) and dissolved nitrogen (N) in nitrite form (NO_2^-), nitrate form (NO_3^-) and ammonium form (NH_4^+). The sum of dissolved N forms was expressed as DIN. Dissolved organic carbon (DOC) was measured by a TOC analyser (TOC-V CSH, Shimadzu Corporation, Japan). The concentration of soluble reactive phosphorus (SRP) was determined by a colorimetrically discrete analyser (Alliance Instruments Smartchem 140, AMS, France).

To characterize land uses, a sub-basin at each site was delineated from a digital elevation model at a 25-m resolution by computing the flow direction and using a watershed tool with geospatial-processing software (ArcMap 10, ArcGIS, USA). The percentages of simplified land-use cover (urban, natural and agricultural land uses) adapted from Corine Land Cover 2018 were calculated at each site.

The average of canopy cover percentage at each site was calculated using a spherical densitometer (Lemmon, 1956), taking four measures (upstream, downstream, right side and left side of the site) at three points of each site.

Decomposition rates and fungal biomass

To calculate decomposition rates, 10 tongue depressor sticks of Canadian poplar wood (*Populus x canadensis*) (15 × 2 × 0.2 cm) (Arroita et al., 2012) were placed in the riverbed at each site in November 2018. All wood sticks were previously marked, oven-dried (70°C, 72 h) and weighed. Five wood sticks were collected after 90 days, and the other five were collected after one year of incubation. Sticks were placed in zip-lock

Table 3.1. Land uses, flow intermittence, canopy cover and chemical water characteristics in the studied reaches. Percentages of land use cover refer to the total sub-basin area associated with each site. Urb. = urban, Agr. = agricultural, and Nat.= natural land uses. DOC= dissolved organic carbon. DIN = dissolved inorganic nitrogen. Values (Mean ± SE) are the mean of the four field campaigns. NA: only one value was available to calculate the mean. Site E11 was always dry when we went to the field.

Site	Catchment land–uses (%)			Flow intermittence				Canopy cover (%)	Chemical water characteristics						
	Urb.	Agr.	Nat.	Non-flow periods	Flow periods	Non-flow days	Flow days		Mg (mg Mg/L)	Ca (mg Ca/L)	DOC (mg C/L)	DIN (µg N/L)	Conductivity (µS/cm)	DO (%)	pH
E10	0	33.41	66.59	4	3	148	222	59.4 ± 6.4	4.6 ± 4.3	30.5 ± 9.0	22.1 ± 7.2	999.8 ± 422.6	311.3 ± 20.2	81.4 ± 6.2	8.5 ± 0.1
E11	0	0	100	0	0	370	0	26.6 ± 3.9	-	-	-	-	-	-	-
E12	0	0	100	0	0	0	370	25.8 ± 5.3	7.0 ± 6.5	43.4 ± 11.1	54.0 ± 18.2	218.8 ± 14.8	522.5 ± 36	65.2 ± 1.3	7.9 ± 0.2
E13	0	33.41	66.59	1	1	108	262	13.5 ± 1.1	7.9 ± 7.4	40.8 ± 8.7	56.2 ± 27.3	231.7 ± 46.9	489.3 ± 34.9	107.0 ± 4.4	8.8 ± 0.3
E14	0	33.41	66.59	2	2	105	265	35.4 ± 2.6	6.2 ± 5.7	34.5 ± 8.2	41.7 ± 20.1	247.7 ± 74.1	414.2 ± 47.3	87.3 ± 3.7	8.7 ± 0.2
E15	0	0.21	99.79	1	1	316	54	26.3 ± 4.6	12.2 ± NA	43.9 ± NA	2.9 ± NA	109.0 ± NA	297.2 ± 43.9	85.2 ± 12.0	8.6 ± 0.2
E16	0	33.41	66.59	1	1	19	351	1.0 ± 0.4	5.0 ± 4.3	30.0 ± 2.4	32.6 ± 11.4	4287.0 ± 1941.9	420.6 ± 18.6	91.8 ± 4.4	8.8 ± 0.1
A1	0	3.10	96.90	0	0	0	370	7.0 ± 2.9	5.8 ± 5.4	35.9 ± 9.1	30.0 ± 9.9	177.5 ± 52.9	360.4 ± 18.5	95.3 ± 3.0	9 ± 0.1
A2	0	3.10	96.90	0	0	0	370	29.7 ± 2.5	4.8 ± 4.4	31.1 ± 9.6	25.6 ± 8.8	105.3 ± 28.1	325 ± 27.3	86.4 ± 3.9	8.9 ± 0.1
A3	0	3.10	96.90	1	1	55	315	2.6 ± 2.3	6.6 ± 6.0	37.3 ± 10.0	34.4 ± 11.0	569.8 ± 359.8	395.3 ± 32.1	87.8 ± 4.2	8.3 ± 0.6
A4	0	73.33	26.67	0	0	0	370	0.0 ± 0.0	7.2 ± 6.2	38.9 ± 9.7	34.9 ± 11.2	5261.5 ± 1291.5	434.8 ± 27.6	90.9 ± 5.9	8.9 ± 0.1
A5	0.01	57.57	42.42	0	0	0	370	5.7 ± 2.5	7.5 ± 6.0	45.3 ± 10.9	40.8 ± 13.2	3770.3 ± 1461.9	442.5 ± 35.6	100.8 ± 4.5	9.1 ± 0.1
A6	0.01	57.57	42.41	1	1	20	350	0.0 ± 0.0	9.9 ± 8.2	46.5 ± 12.4	33.9 ± 15.9	3881.0 ± 1377.5	427.4 ± 58.7	100.0 ± 6.2	9 ± 0.1
A7	0.45	47.79	51.76	0	0	0	370	0.0 ± 0.0	10.4 ± 8.7	48.6 ± 12.3	32.2 ± 14.9	2810.0 ± 1413.3	470.1 ± 31.9	83.0 ± 10.9	8.8 ± 0.1
A8	0.45	47.79	51.76	3	2	179	191	0.0 ± 0.0	11.8 ± 9.9	55.7 ± 10.8	44.7 ± 21.1	2031.3 ± 1206.0	986.1 ± 473.3	87.0 ± 7.8	8.8 ± 0.3
A9	0.24	46.73	53.02	2	2	169	201	4.9 ± 2.0	13.5 ± 10.0	68.7 ± 8.0	101.0 ± 56.6	3645.3 ± 955.4	1086.9 ± 346.2	81.8 ± 12.8	8.5 ± 0.4

bags and transported to the laboratory in refrigerated containers. To avoid ergosterol degradation and changes in weight, wood sticks were processed immediately in the laboratory. First, wood sticks were brushed to remove adhered material and washed with distilled water. Later, an aliquot of 1 cm of each stick was cut and frozen at -80°C for later determination of ergosterol concentration as a proxy of fungal biomass (Gessner, 2005). The remaining part of each wood stick was dried (70°C, 72 h), weighed and summed to the fraction of the frozen aliquot to measure ergosterol (see below). Then, another 1-cm-long aliquot of each wood stick was cut and incinerated (500°C, 5 h) to remove inorganic components and to determine the AFDM. The initial AFDM was determined from an extra set of 20 sticks. This set was also transported into the field but not placed in the river and returned to the laboratory, which was processed as described above to calculate a conversion factor between the initial air-dry mass and the initial AFDM, considering manipulation losses.

To determine ergosterol concentration, frozen aliquots of each wood stick were lyophilized and weighed. Lipid extraction and saponification were performed using 0.14 M KOH methanol (8 g L^{-1}) in a shaking bath at 80°C for 30 minutes. To purify lipid extractions, solid-phase extraction cartridges were used (Waters Sep-Pak® Vac RC, 500 mg tC18 cartridges, Waters Corp, Milford, MA, USA), and ergosterol was eluted using isopropanol. High-pressure liquid chromatography (HPLC; Jasco HPLC system, USA) was used at 282 nm to detect and quantify ergosterol using a Gemini-NX 5 µm C18 250 × 4.6 mm column (Phenomenex, UK). The ergosterol measurement was converted into fungal biomass using a conversion factor of 5.5 mg of ergosterol per gram of fungal mycelium (Gessner and Chauvet, 1993). The results were expressed as mg of fungal biomass per gram of dry mass.

Decomposition rates were calculated following the negative exponential equation $M_t = M_0 \cdot e^{-kt}$, where M_0 is the initial percentage of AFDM, M_t is the remaining AFDM at time t, k is the decay rate, and time t was replaced by the mean daily temperatures accumulated to express decay rates in degree days (dd^{-1}), i.e., in terms of accumulated heat (Stout, 1989). The mean daily temperatures were obtained from leveloggers.

Data analysis

To explore the environmental variables jointly and their relationships with sites, Principal Components Analysis (PCA) was performed. All environmental variables, including flow intermittence descriptors, were used. This analysis will also allow us to assess the relationship between variables.

To analyse how flow intermittence and environmental characteristics affected the decomposition rates, automated model selection for the linear regression model was performed using the R package MuMIn (Barton, 2009) to select the best combination of all predictor variables based on AICc (Akaike Information Criterion corrected version for small samples). To assess collinearity between explanatory variables, pairwise Pearson correlations and the variance inflator factor (vifstep of usdm R Package) (Feld et al., 2016) were previously estimated. Therefore, agricultural land uses (highly correlated with DIN^3 concentration), conductivity (correlated with Ca and DOC) and Mg (correlated with Ca) were discarded (Table S3.2). Then, the final set of explanatory variables tested in the automated model included the annual means of seasonal variables (DIN, Ca and DOC), flow intermittence variables (non-flow periods and non-flow days) and basin descriptors (canopy).

To analyse the effects of flow intermittence and environmental characteristics on fungal biomass, automated model selection for the mixed linear model was performed using the R package *MuMIn* (Barton, 2009) to select the best combination of predictors. Fungal biomass values at two sampling times (90 and 365 days) were used considering time as a fixed effect factor, while site was considered a random effect factor. For these analyses, the averages of seasonal variables (DIN, Ca, Mg, DOC, water temperature and conductivity) and flow intermittence variables (non-flow periods and non-flow days) were calculated at 90 and 365 days (Table S3.2). To assess predictor collinearity, the same previous methodology explained above was conducted. Here, DIN, non-flow days, Ca, water temperature, conductivity and canopy were included in the analysis.

To relate fungal biomass to decomposition rates, linear regression was performed. The linear model assumptions were assessed and verified for all models performed (Poole and O'Farrell, 1971). The distribution of all variables was explored before the statistical analysis. All explanatory variables, except non-flow periods,

were squared-root-transformed. Decomposition rates (k_{dd}) and fungal biomass were log-transformed. All variables were finally Z-standardised (mean = 0, SD = 1) to facilitate model coefficient comparison and avoid the influence of the measurement units in PCA. All statistical analyses were performed using R software (R Core Team, 2020).

RESULTS

Environmental characteristics

The Algars river presented permanent, intermittent and dry sites across the basin (Table 3.1). Intermittent sites presented great variability in intermittence intensity in the studied period. Specifically, for intermittent sites, non-flow days varied between 19 and 315 days, with a mean of 124 days, and non-flow periods varied between 1 and 4, with a mean of 1.8. Water characteristics were variable across sites (Table 3.1 & Table S3.1). Magnesium (4.5 – 13.4 mg L^{-1}), calcium (30.0 – 68.7 mg L^{-1}), DOC (2.9 – 101.0 mg L^{-1}), and conductivity (297.2 – 1086.9 µS cm^{-1}) showed a similar trend, increasing downstream except in the Estrets stream. The percentage of dissolved oxygen presented values between 66.1 and 107.0, where E12 had the lowest value and E13 the highest (Table 3.1). The pH varied between 7.9 and 9.0. Dissolved inorganic nitrogen (DIN) was used as representative of all nitrogen forms and varied between 105.3 and 5261.5 µg L^{-1}. The main dissolved nitrogen form was nitrate and was related to agricultural practices in each sub-basin. For instance, the concentration of DIN at site A4 was the highest, which was also the site with the highest percentage of agricultural land use (73.3%). Canopy cover varied between 0 and 59%, which was related to headwater sites and smaller width of the streambed.

The first two components of PCA with the environmental variables explained almost 70% of the total variance. (Table S3.3). Specifically, PC1 explained 43.31%, while PC2 explained 26.08% (Figure 3.2). PC1 indicated environmental characteristics and separated headwater sites (Estrets and Algars headwater streams) characterized by lower conductivity and a higher percentage of canopy than downstream sites (Algars after the confluence). PC2 separated sites according to flow intermittence measures and agricultural land uses (Table S3.4). However, intermittent sites with low non-flow days (E16, A3 and A6) were situated next to permanent sites because these sites were

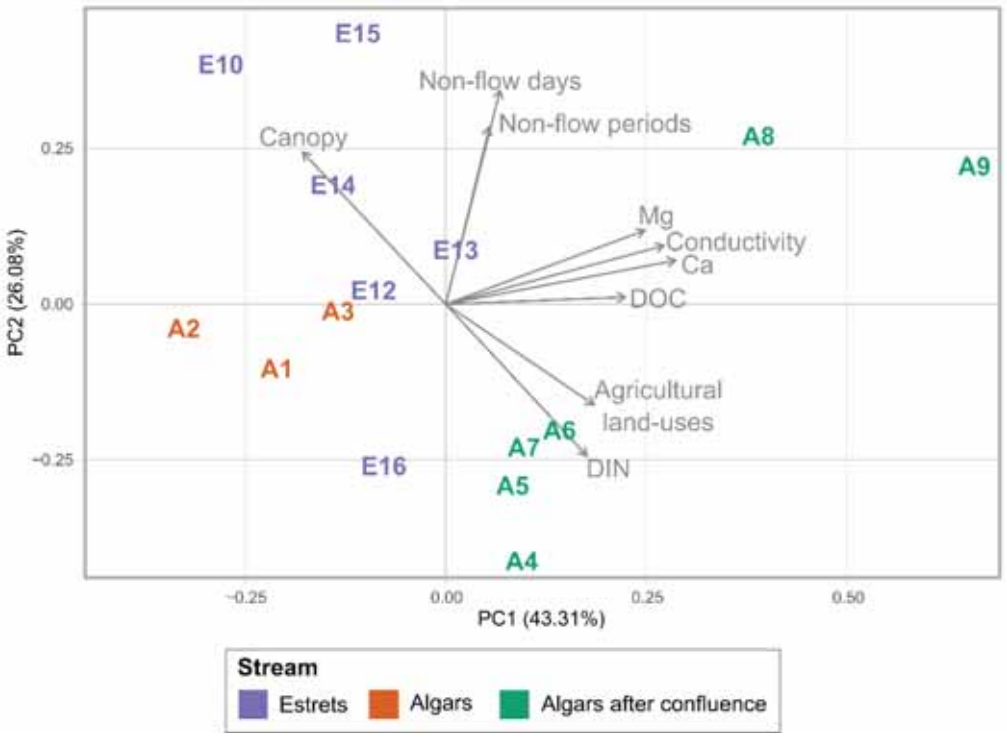


Figure 3.2. PCA biplot representation using PC1 (43.3% variability) and PC2 (26.1% variability). Sites are represented by their names and with colours of their respective streams (purple for the Estrets stream, orange for the Algars stream before the confluence, and green for the Algars sites after the confluence). The grey arrows represent the component weights and allow us to understand the relationship between variables and principal components.

characterized by low canopy cover and high DIN concentrations. On the other hand, permanent sites A4 and A5 were characterized by high DIN concentrations and a great proportion of agricultural land uses, while sites E12, A1 and A2 were permanent but with a high percentage of natural land uses and low DIN concentrations.

Decomposition rates

Decomposition rates (k_{dd}) varied between $9.2 \cdot 10^{-6}$ and $4.1 \cdot 10^{-4}$ dd^{-1} (Figure 3.3A; Table S3.5). The highest values corresponded to A4 and A5 ($2.4 \cdot 10^{-4}$ and $4.1 \cdot 10^{-4}$, respectively), sites located downstream, permanent sites and sites with the highest DIN concentration. The lowest values corresponded to E11, E15 and A8 ($9.2 \cdot 10^{-6}$, $1.8 \cdot 10^{-5}$ and $1.7 \cdot 10^{-5}$, respectively), sites with the highest duration of intermittence (370, 316 and 179 days, respectively). The results of model selection showed that k_{dd} was

associated with DIN, canopy and non-flow days (adjusted R^2 = 0.58; $F_{3,11}$ = 7.35; p-value = 0.006). All variables were significant (Table S3.6). DIN and canopy had a positive coefficient, which implies an increase in k_{dd} with higher values of DIN and canopy. However, non-flow days had a negative coefficient, which indicates a decrease in k_{dd} with higher values of non-flow days.

The percentage of AFDM lost increased between 15 and 55% due to the DIN effect (Figure 3.4) depending on the hydrological regime. For instance, permanent sites with low DIN concentrations (A1, A2 and E12) had AFDM losses of 12.2%, 18.0% and 20.1%, respectively, while A4 and A5, permanent sites but with 30 times more DIN, had the highest AFDM losses (56.8% and 66.8%, respectively). In intermittent reaches, sites with a high DIN (E10, A6 and A9) had a higher AFDM loss (39.7%, 27.6% and 24.9%, respectively) than sites with a low DIN (E13, E14 and E15 with 13.0%, 11.1% and 6.9%, respectively). Then, the effect of non-flow days was clear on E12, E13 and E14 with low DIN concentration values, and AFDM loss decreased almost 20% with an increase in non-flow days. However, E11, E15 and A8, with different DIN concentrations, had a similar AFDM loss because the severity of intermittence was the highest at these sites. In addition, an increase of 20% of canopy meant increases next to 5% of AFDM lost. For example, A1 and A2 were permanent sites with similar DIN concentrations and 7.0% and 29.7% of the canopy, respectively. A2 presented 6% more AFDM loss than A1. Another example was intermittent reaches E10 and E16: E16 had 76.7% higher DIN concentrations, 129 non-flow days less and 58.3% less canopy cover than E10, but E10 had 19.1% more AFDM loss than E16.

Fungal biomass

Fungal biomass associated with wood litter varied between 2.8 and 294.8 µg/g AFDM (Figure 3.3B; Table S3.7). In general, the one-year fungal biomass presented greater variability and values than that observed after three months of incubation. A linear and positive relationship was found between the logarithm of decomposition rate and fungal biomass (adjusted R^2 = 0.55; $F_{2,25}$ = 17.64; p-value < 0.0001; Table S3.8; Figure S3.1).

The model obtained with model selection showed that the fungal biomass was related to DIN, canopy, non-flow days and extraction days (conditional R^2 = 0.70). DIN,

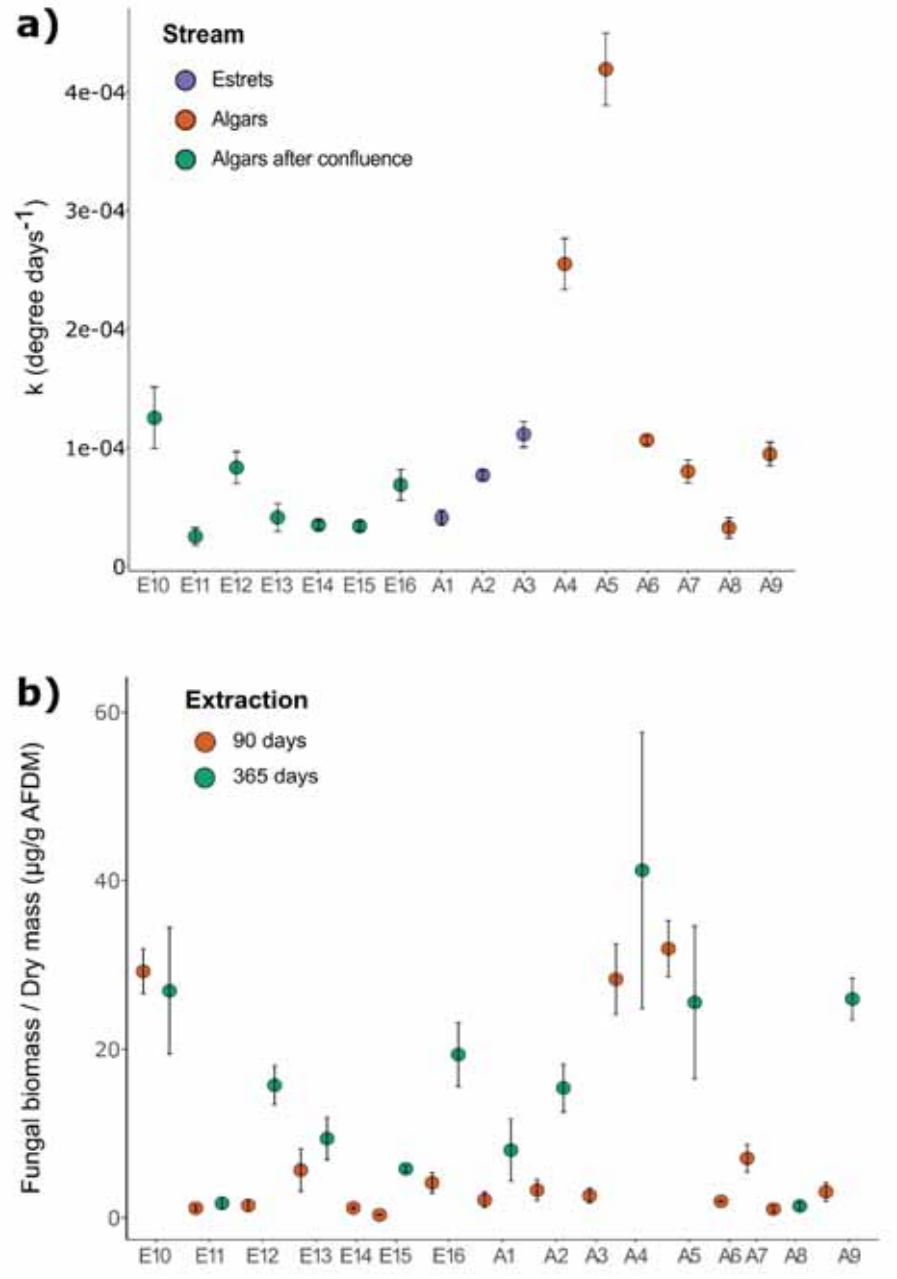


Figure 3.3. a) Mean plot of decomposition rates at all study sites of the Algars river basin. Decomposition rates are in degree days -1. Colours correspond to the respective streams of each site (purple for the Estrets stream, orange for the Algars stream before the confluence, and green for the Algars sites after the confluence). b) Mean plot of fungal biomass at each site and at each extraction. Orange colour corresponds to the 90-day extraction, and green colour corresponds to the 365-day extraction. All dots represent the means, while the bars represent standard error.

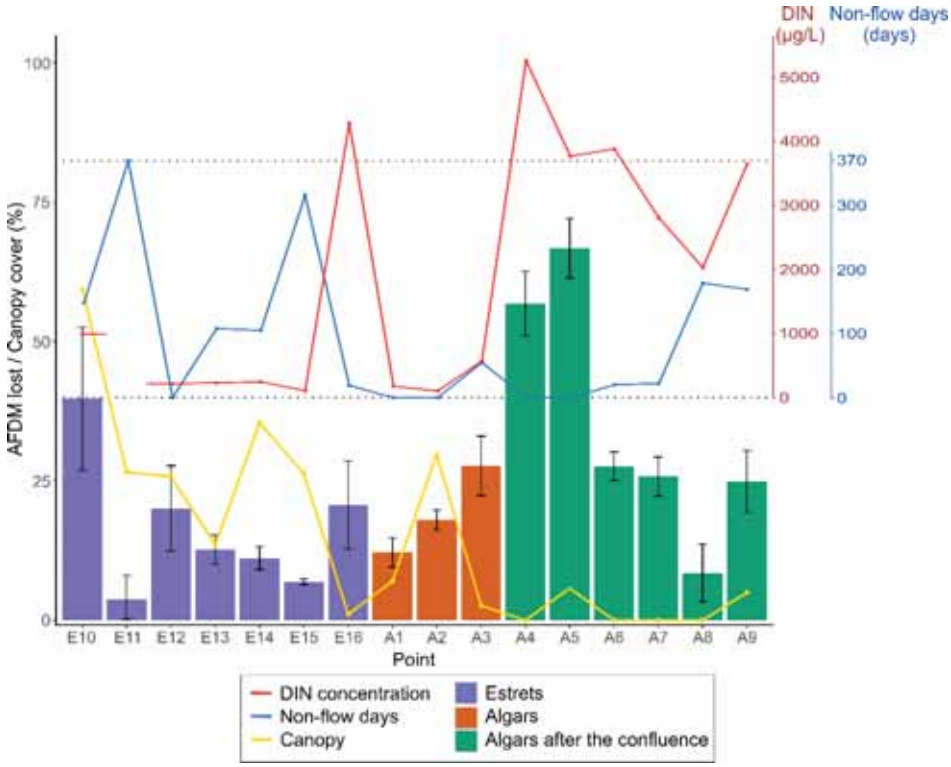


Figure 3.4. Barplot of percentage of mean of ash free dry mass (AFDM) lost, filled with colours that correspond to their respective streams (purple for the Estrets stream, orange for the Algars stream before the confluence, and green for the Algars sites after the confluence). The yellow line is the percentage of canopy cover at each site. The blue line corresponds to the total number of non-flow days at each site. The red line is the mean DIN concentration at each site (µg N/L). Vertical bars represent the standard errors.

estimated parameters of canopy cover and extraction days were significant and showed a positive coefficient (Table S3.9), which implies an increase in fungal biomass related to incubation time at higher DIN concentrations and canopy cover. The estimated parameter of non-flow days was marginally significant (p-value = 0.069) and had a negative coefficient, indicating a decrease in fungal biomass with an increase in non-flow days.

DISCUSSION

The distribution of land uses in the basin reveals interactive effects with flow intermittence on OM decomposition. We hypothesized that an increase in intermittence intensity negatively affected the decomposition rates in the study basin. Our results

confirmed this prediction, and the sites with more than 170 days of flow cessation showed the lowest decomposition rates. Non-flow days were one of the predictors of the decomposition dynamics selected by the linear model with a negative effect. This effect was counteracted by the presence of nutrients (DIN) coming mainly from agricultural activity and, with a lower intensity, from canopy cover, which was not expected in our initial hypothesis.

In natural reaches (without anthropogenic activities), intermittence reduced the processing of OM (measured as AFDM) by a mean of 14.9% in comparison with permanent sites, and this reduction was higher with an increase in intermittence duration, as previous studies found (Corti et al., 2011; Datry et al., 2011). As flow fragmentation is variable along the river, spatial and temporal habitat heterogeneity creates different ecological conditions that result in a diverse decomposition process in accordance with the prevailing environmental conditions (Abril et al., 2016). For instance, in dry streambeds, such as site E11, the decomposition process is terrestrial with lower mass losses because terrestrial detritivores are scarce and microbial activity declines (Maamri et al., 1997; Corti et al., 2011). Thus, OM decomposition is faster in aquatic systems than in terrestrial systems due to enhanced leaching, microbial metabolism, and aquatic invertebrate activity (Mora-Gómez et al., 2020).

Intermittence intensity was measured by non-flow days and the number of dry periods, but only non-flow days were a selected predictor for decomposition rates and fungal biomass. The first variable could be considered a measure of the duration of the flow interruption, while the second could be considered a measure of its frequency (Langhans and Tockner, 2006). Coinciding with our results, previous studies found that the duration of dry periods had more influence on OM decomposition than their frequency because the activity of aquatic decomposers decreased with a reduction in flow, but they quickly recovered their activity after rewetting (Pohlon et al., 2013; Foulquier et al., 2015; Niyogi et al., 2020), especially microbial decomposers, considering that aquatic invertebrates take slightly longer to recolonize the reach (Corti et al., 2011).

In Mediterranean rivers, the drying phase is a scaled and prolonged process during the summer period, while the resumption of flow is usually faster across the network during autumn (Vazquez et al., 2013; Boulton et al., 2017). Our results showed an

increase in fungal biomass with time, which suggested a fast recovery of fungi after autumnal rewetting. However, during the drying phase, aquatic decomposer communities were affected by changes in environmental conditions in different ways. For instance, isolated pools characterized by a decrease in water flow and low oxygen and detritus accumulation were harsh habitats for fungi (Canhoto et al., 2016), while these conditions did not affect bacteria. Abril et al. (2016) found a decrease in fungal biomass in isolated pools during the drying phase compared with running waters, while bacterial biomass did not show differences between these habitats. In any case, the presence of water determines the continuity of the processing of OM by microbial assemblages, and when water disappears, this process practically stops. Even so, previous studies showed that fungi could be less sensitive to severe drought than bacteria (Maamri et al., 2001; Duarte et al., 2017). In our study, the close relationship between decomposition rates and fungal biomass would suggest that fungi were the main driver of wood decomposition and that their responses to flow variability (although marginally significant in the model) could explain differences in OM processing in the studied basin.

On the other hand, and as we hypothesized, agricultural land uses increased water nutrient enrichment in streams, which positively affected OM decomposition rates. A positive effect of water nutrient enrichment was also observed in relation to fungal biomass. For instance, Abril et al. (2015) identified a unimodal distribution of decay rates related to total agricultural land use in summer in a Mediterranean basin, when temperature and nutrient concentrations increased. In addition, they found that high order reaches presented lower decay rates and less variability between winter and summer than low order reaches, where agricultural practises had a greater presence. These results are consistent with previous studies (Stelzer et al., 2003; Gulis et al., 2004). Fungi have the capability to use inorganic nutrients from water, especially when they colonize a poor-quality substrate, such as wood, which is rich in lignin with a high ratio of C:N (Suberkropp, 1998; Sridhar and Barlöcher, 2000; Stelzer et al., 2003; Ferreria et al., 2006). The predominant form of DIN in the study basin was nitrate (Table S3.1), which is associated with anthropogenic activities, especially with agricultural practices (Lassaletta et al., 2009), and it could cause a significant change in decomposition rates and fungal biomass with small increases (Ferreira et al., 2006).

Our results suggested that DIN concentration modulated the negative effects of the duration of flow intermittence: the presence of DIN favoured OM processing. For instance, at sites with a similar number of non-flow days, the processing of OM was up to three times lower with low DIN concentrations, while the processing of OM when comparing permanent and intermittent reaches was reduced almost two times at sites with high DIN concentrations. However, if the severity of the intermittence increased, the effect of DIN seemed to be insignificant. This interaction between factors existed across the basin, especially at downstream sites, where agricultural practices were more important.

Additionally, our results showed that the percentage of canopy cover also affected decomposition rates and fungal biomass. Canopy cover is related to forestry land uses extending to headwater sites, where fungi are considered the main decomposers of leaf litter and bacteria play a secondary role (Hieber & Gessner, 2002). This could justify the differences found in decomposition rates and fungal biomass at headwater sites with similar durations of intermittency and low DIN concentrations. High canopy cover implies an entry of allochthonous leaf litter, which could stimulate fungal biomass and their activity (Gessner et al., 1999). Canopy cover reduces sunlight incidence, especially ultraviolet radiation (UV), which has direct effects on fungal development (Newsham et al., 1997). The decrease in light availability limits the growth of algal biofilms, reducing competition with fungi for inorganic nutrients (Daufresne and Loreau, 2001). Algal biofilms are also an indirect competitor for fungal decomposers because algae are a more nutritive resource than leaf litter for invertebrates (Tonin et al., 2018). In summary, light affects microbial assemblages in streams, limiting fungal development, favouring algae and having low or no effect on bacteria (Albariño et al., 2008), but other authors have also considered that algae stimulate the presence of bacterial decomposers (Danger et al., 2013), maintaining the processing of OM, especially in downstream sites. All this will have an effect on the processing of OM in streams. For instance, site E16 presented a high light incidence, which explained the presence of a high density of filamentous algae (personal observation), which could be related to the low decomposition rate and fungal biomass observed, even with a high DIN concentration. However, the effect of canopy cover was

clear only in headwater reaches, where this factor showed variability, but not downstream, where all sites were open and unshaded.

Fungal biomass explained more than 50% of the decomposition rates in the study basin. Nevertheless, the site with the highest decomposition rates (A5) did not have the highest fungal biomass, and other biotic components affected decomposition processes in the Algars basin. Previously, we mentioned the competition between microbial communities (algae, fungi and bacteria) related to nutrients and light availability, but in addition to this permanent site, we observed a high density of American crabs (*Procambarus clarkii* Girard, 1852), which fragmented the wood sticks, causing mass loss. *Procambarus clarkii* is an invasive species on the Iberian Peninsula with high plasticity to environmental variability (Geiger et al., 2005) but is usually found in downstream reaches with low riparian quality and eutrophication (Maceda-Veiga et al., 2013).

Flow intermittence affects OM decomposition and fungal biomass in the entire basin, but the drying phase is variable across the river network and time, resulting in differences in flow disruption and its duration. The mosaic between terrestrial and aquatic habitats and the duration of flow interruption imply great variability in the quantity of processed OM and the potential for its transport among the habitats, which was not studied here. In addition, land uses and human activities, such as water nutrient enrichment, also affect the decomposition process in the entire basin, but this effect is related to local impacts and their position in the river network. However, as a generalization, agricultural land uses were located on downstream and forested streams on headwater. Even so, local characteristics are important in explaining the differences across the basin in the processing of OM and in the global budget of carbon in receiving downstream waters (Del Campo et al., 2021).

CONCLUSIONS

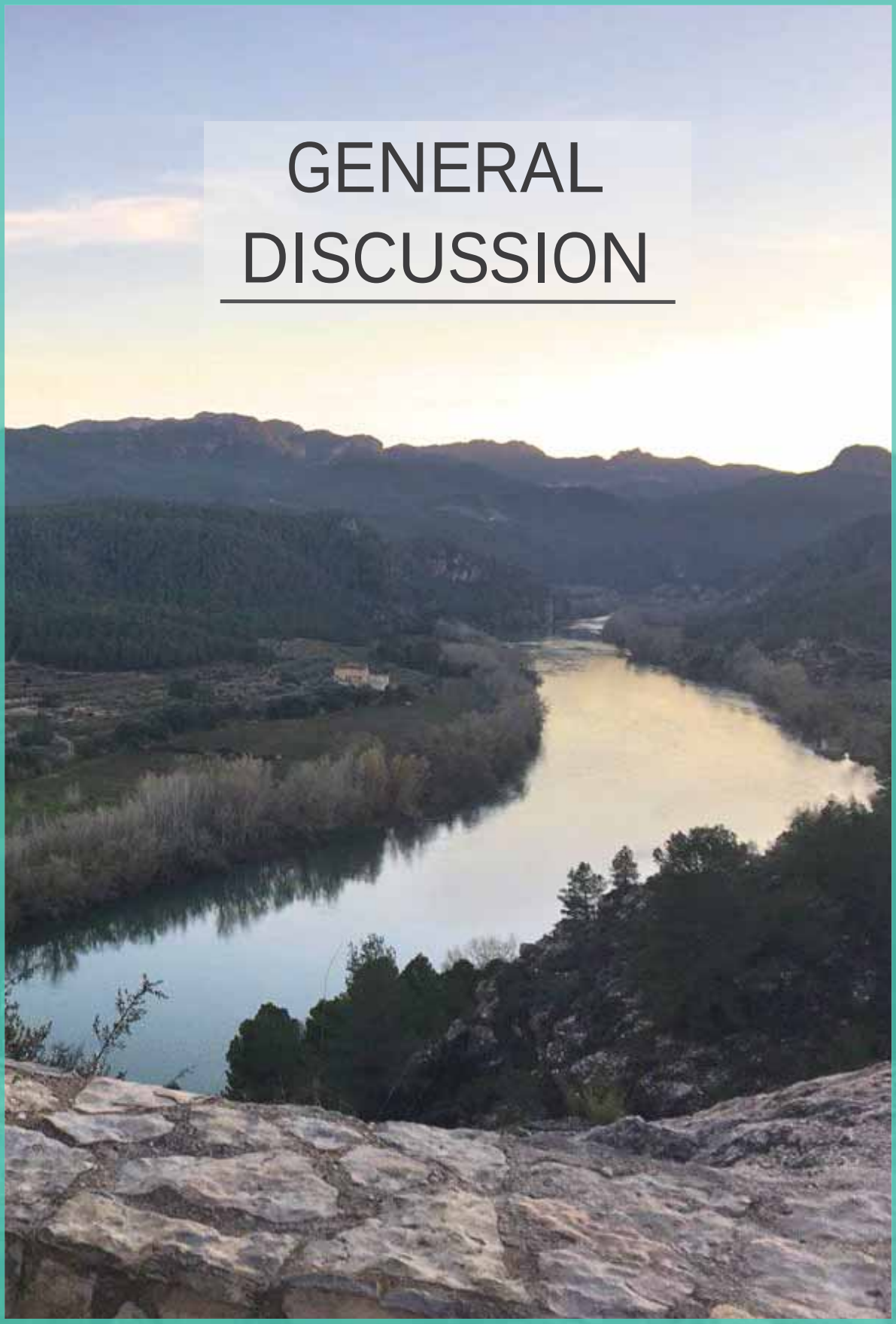
This study demonstrated the negative effect of the duration of flow intermittence on OM decomposition, and how interacted with other local environmental factors across the river basin. An increase in the intensity of flow intermittence reduced OM decomposition, but water nutrient enrichment – favoured by agricultural activities –

and canopy cover – related to forested headwaters – counteracted this effect. Nutrients artificially accelerate natural OM processing in the study basin and canopy cover also have a positive effect on OM processing. However, if the severity of the intermittence increased, the effect of counteracted factors seemed to be insignificant. Flow intermittence is a natural perturbation in Mediterranean rivers, but its intensification and increase to other regions is expected to be a consequence of climate warming and an increase in freshwater demand. In the current context of global change, it is especially relevant to further investigate the interactions between flow intermittence and other factors on OM processing at the basin scale to incorporate these data into the global carbon dynamics in IRs. Locally, our results will help to preserve natural resources in the study basin, as well as to improve river management, maintain natural uses in headwaters to guarantee the role of riparian forests as a source of OM inputs, limit light and stimulate microbial decomposition, and control nutrient inputs from agricultural downstream areas.

Acknowledgements

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GENERAL DISCUSSION



“Growth for the sake of growth is the ideology of the cancer cell”

– Edward Abbey,
The Journey Home: Some Words in Defense of the American West

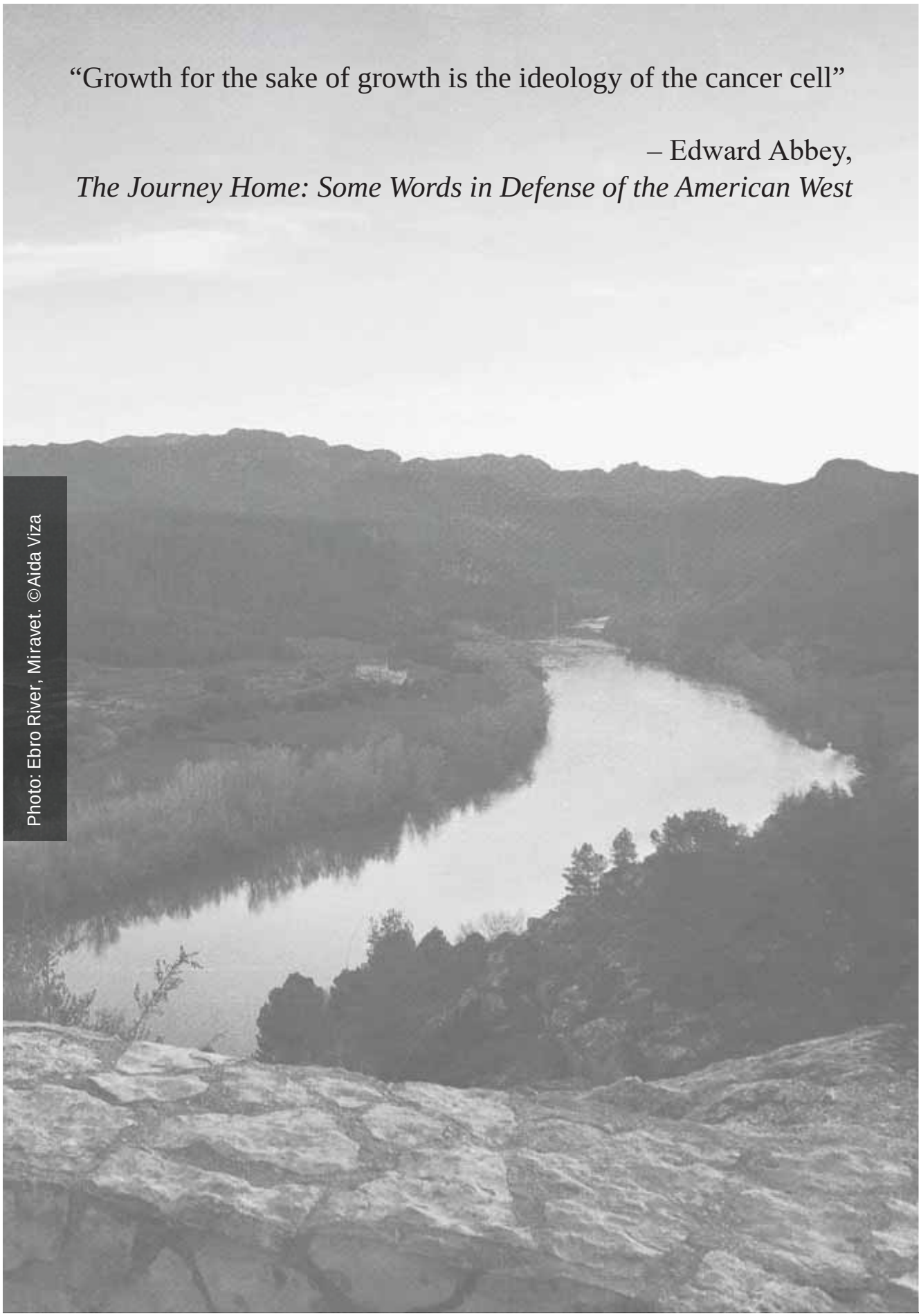


Photo: Ebro River, Miravet. ©Aida Viza

General Discussion

Intermittent River and Ephemeral Stream (IRES) have gained significant attention as they constitute over 50% of global fluvial networks (Messager et al., 2021). The spatial and temporal extension of IRES is increasing in many regions due to anthropogenic activities and climate change (together, global change) (Datry, Boulton, et al., 2018). Natural IRES show a range of species diversity, with organisms specifically adapted to either withstand dry conditions *in situ* (resistance) or to promptly recolonise when water flow resumes (resilience) (Bogan et al., 2017). Nevertheless, questions remain about the efficacy of these strategies in the recovery of species diversity upon flow resumption as well as their vulnerability under current climate change scenarios.

Although the patterns of invertebrate diversity and ecosystem functioning in IRES have been extensively studied (Bogan et al., 2013; Lake, 2000; Leigh & Datry, 2017), our understanding of the combined effects of natural drying processes and anthropogenic impacts remains limited. Moreover, the lack of a comprehensive consideration of entire stream networks in ecological studies may limit our insight into the broader impacts, thereby constraining effective management and conservation strategies. Mediterranean small stream networks, characterised by their inherent variability in flow dynamics (Bonada & Resh, 2013) that are influenced by both climate and anthropogenic factors and compounded by soil degradation caused by recent changes in land use (Ruiz & Sanz-Sánchez, 2020), serve as ideal subjects for this research. This knowledge can be extended to 'new' intermittent streams, resulting from the spatiotemporal expansion of drying due to climate change and water exploitation.

This thesis contributes to the current knowledge of the impact of both drying and different land uses on the diversity and functioning of IRES by providing further information on the diversity of aquatic invertebrates and the decomposition process of terrestrial organic matter (OM) throughout a hydrological year in a Mediterranean stream network. This network encompasses protected forested upstream headwaters and downstream areas impacted by agriculture. A pivotal focus of this thesis is the survival strategies of aquatic invertebrates in various Mediterranean streams, such as migration to hyporheic zones or the occurrence of a desiccation-tolerant stage. In the

following discussion, I synthesize the results from the chapters of this thesis. My aim is to provide an overarching view, compare these results with the initial hypotheses, elucidate their implications, and suggest avenues for future research to address unresolved questions. Overall, my research reveals that flow intermittence negatively impacts the diversity of aquatic invertebrates, OM decomposition, and its associated fungal biomass across the entire stream network. Notably, while forested headwater streams are less affected by drying in terms of the diversity of aquatic invertebrates, agricultural activities appear to mitigate the effects of drying on OM decomposition.

The discussion is organised into three main sections. The first section exclusively examines the impact of drying on the diversity of aquatic invertebrates and OM decomposition at both the stream network and reach scales. The second section focuses on the combined effects of drying and different land uses on the diversity of aquatic invertebrates and OM decomposition. Finally, the concluding section centres on the implications of global change scenario for IRES, with future research directions and unresolved questions within this context also provided.

Effects of drying on aquatic invertebrate diversity and OM decomposition at the reach and network scale

The diversity of aquatic life and the functioning of streams are intricately linked to the prevailing flow regimes. Under flowing conditions, aquatic invertebrate communities colonise the streambed, while OM decomposition is governed by factors and processes similar to those in perennial watercourses. However, during drying at the reach scale, the taxonomic richness of aquatic invertebrates diminishes due to flow reduction and fragmentation, with the desiccation-sensitive taxa disappearing (Stubbington, Bogan, et al., 2017). Concurrently, OM decomposition slows down and begins to accumulate on the streambed (Datry, Foulquier, et al., 2018). During dry phases, aquatic invertebrates are compelled to survive in the remaining wet habitats, such as remnant pools, and the emerged OM is influenced by various abiotic factors, including solar radiation and precipitation (Figure I.4; Arscott et al., 2010; Del Campo et al., 2021). With an increase in the duration and frequency of drying events, conditions in wet refuges can deteriorate due to water content loss and changes in

physicochemical characteristics, affecting both the survival of taxa and the processing of aquatic OM (Arias-Real et al., 2020; Stubbington, Bogan, et al., 2017). The duration of the dry periods, followed by rewetting periods, plays a pivotal role in determining aquatic invertebrate diversity and the rate of OM decomposition (Larned et al., 2010).

Aquatic communities exhibit diverse adaptation levels to a range of flow perturbations, encompassing drying and floods (see references in Chapters 1 and 2). Distinct traits enable these organisms to resist and recover from drying. For instance, some organisms possess desiccation-tolerant life stages and seek refuge in hyporheic zones, enabling them to withstand dry phases *in situ* (see Chapter 2). In the Algars, the invertebrates in hyporheic zones and invertebrate seedbanks during dry phases show generalist feeding habits and small body sizes. The hyporheic assemblage is also characterised by the capacity to migrate to hyporheic zones, while the seedbank assemblage is noted by resistance forms' traits, similar to that reported for other studied streams (Chapter 2). Both hyporheic and seedbank assemblages also present a high abundance of resilience traits, such as the terrestrial adult stage, showing that almost all the individuals present in a hyporheic zone during a dry phase are likely be larvae. These resilience traits, including the dispersal capabilities of the adult stages, aid in the swift recolonisation once the flow is re-established (Bogan, Chester, et al., 2017).

The decomposition of OM, primarily of a terrestrial origin, is a crucial process in the functioning of many stream ecosystems, with notable implications for global biogeochemical cycles. In Chapter 3, tongue depressors crafted from *Populus x canadensis* wood were used to investigate OM decomposition during a hydrological year in the intermittent stream network of the Algars. Employing wooden sticks as a substrate provides a rapid, straightforward, cost-effective, and standardised way of measuring a crucial ecosystem function, showing greater longevity than leaves and other standardised substrates (Arroita et al., 2012), including cotton strips (Colas et al., 2019; Tiegs et al., 2013), tea bags (Mori, 2021), and cellulose filters (Fritz et al., 2011).

While there is extensive literature on the ramifications of drying on ecosystem responses, specifically the diversity of aquatic invertebrates (see references in Chapter 1) and OM decomposition (see references in Chapter 3), the majority of these studies focus on the reach-scale. Although reach-scale studies provide insights into specific

ecological responses (Chapter 2), overlooking the comprehensive stream network compromises our predictive capabilities regarding ecosystem responses to global change (Chapters 1 and 2).

Effects of drying on aquatic diversity

As discussed in Chapter 1, extended drying diminishes both taxonomic and functional α-diversity, aligning with my initial hypothesis. Specifically, longer dry phases negatively impact taxonomic diversity (the Shannon-Wiener index), as well as functional richness and redundancy (Chapter 1). Drying limits the presence of particular taxa within a stream reach, effectively filtering out the taxa that are susceptible to desiccation (Arscott et al., 2010). In the Algars, only seven taxa were identified as negatively affected by drying (Chapter 1). However, all of them display aquatic respiration and the capacity to disperse actively. The first trait relates to the ability to withstand harsh drying conditions, such as low oxygen levels, whereas the dispersal capacity is associated with the ability to recolonise upon flow resumption, demonstrating resilience to drying (Chapters 1 and 2; Bonada, Dolédec, et al., 2007; Robson et al., 2011; Strachan et al., 2015). Additionally, seasonality has a significant influence on both taxonomic and functional α-diversity. In the Algars, taxonomic α-diversity peaks in most reaches between winter and spring, reflecting favourable conditions under continuous flow. By contrast, the lowest values are observed in the summer, during the expected seasonal flow disruptions, followed by autumn. The flow resumption in autumn can result in reduced invertebrate density due to a 'dilution effect', accompanied by displacement and mortality, especially during flood events (Hershkovitz & Gasith, 2013). Functional redundancy also shows the lowest values in the summer. More specifically, functional redundancy increases with moderate levels of drying (Chapter 1), but this increase is not enough to offset the reduction in taxonomic diversity resulting from prolonged dry periods (Crabot, Mondy, et al., 2021). The low levels of taxonomic and functional α-diversity observed in the summer highlight the impact of variable seasonal flows. These variations emphasise the functional adaptations of aquatic invertebrate communities in Mediterranean intermittent streams (Bonada, Rieradevall, et al., 2007).

The seasonal variations in both taxonomic and functional α-diversity, as responses to the hydrological regime, are primarily driven by species turnover throughout the year (Chapter 1). Furthermore, longer dry phases heighten temporal β-diversity among aquatic invertebrates in the intermittent stream network under study, as expected. In intermittent reaches, increased durations of dry phases accentuate differences in taxonomic richness (increased taxonomic β-diversity) due to nestedness and negatively impact seasonal species turnover. As flow decreases, lotic habitats and their associated taxa disappear (Stubbington, Bogan, et al., 2017). For instance, during the late summer survey in Algars, stream reaches with fragmented flow and the remnant pools exhibited the lowest taxonomic α-diversity, while others were completely dry (Chapter 1). On the other hand, functional β-diversity exhibits a positive correlation with drying, primarily driven by the β-replacement component. This component represents the whole functional β-diversity, except in sections that completely dry up during the summer (Chapter 1). Given the traits selected in Chapter 1, which pertain to resistance and resilience to drying, changes in functional β-diversity indicate a community of invertebrates that are well-adapted to predictable seasonal drying (Bonada, Rieradevall, et al., 2007).

Resilience to drying is considered the primary mechanism that enables benthic communities to recover once flow resumes in many IRES (Datry, Larned, Fritz, et al., 2014; Doretto et al., 2020). For example, in Mediterranean streams, traits such as short life cycles and multivoltinism, which are associated with resilience to the seasonality of drying, are common in invertebrate communities (Chapter 2; Bonada, Rieradevall, et al., 2007). In addition, these 'resilience traits' are often linked to strategies that avoid the dry phase in water, such as having a terrestrial adult stage and active dispersal abilities, and are also commonly observed in the stream invertebrates. However, the importance of resistance to drying should not be underestimated (Chapter 2; Bogan et al., 2017; Leigh et al., 2016). Organisms in intermittent streams exhibit traits associated with both resistance and resilience to drying (Chapters 1 and 2). Notably, a generalist feeding habit, considered a 'resistance trait', offers an advantage due to the scarcity of food resources during drying in wet refuges (Chapter 2; Aspin, Khamis, et al., 2019; Burrell & Ledger, 2003). In the Algars, seven taxa have been identified as

negatively affected by the duration of drying, of which six are predators (Chapter 2). While drying can initially favour predation by concentrating prey in wet refuges such as remnant pools, prolonged dry periods during flow contraction have a detrimental impact (Chapter 2; Bogan et al., 2013; Bogan & Lytle, 2011). Although some of these taxa exhibit a resistant life stage, they were not found in the hyporheic refuges or invertebrate seedbanks studied in Chapter 2. Additionally, almost all of these taxa possess an adult terrestrial stage, the capacity for active dispersal, and short life cycle durations, suggesting a life cycle adaptation with synchronization between aquatic life stages and flowing phases (Stubbington, Bogan, et al., 2017). Moreover, other resistance traits, such as small body sizes, desiccation-tolerant life stages, and the ability to inhabit hyporheic zones, are also notably present in the invertebrates of other Mediterranean intermittent streams (Chapter 2; Bonada, Rieradevall, et al., 2007).

The use of the hyporheic zone by benthic invertebrates during dry phases can account for up to 40% of the benthic assemblages in the Mediterranean streams studied, with the highest proportion observed in the Algars reach. Moreover, invertebrate assemblages emerging from rehydrated dry sediments during the dry phase can account for up to 16% of these assemblages (Chapter 2). Thus, hyporheic and seedbank assemblages represent subsets of the benthic assemblages, as hypothesised. The presence of wet refuges like the hyporheic zones tends to increase downstream due to an increased geomorphological complexity, a higher mean annual discharge, and enhanced interactions between surface water and groundwater (Sarremejane et al., 2022).

Contrary to my hypothesis, Chapter 2 shows that only the resilience traits of the hyporheic and seedbank assemblages decreased with the prolongation of the dry phase. The availability of *in situ* refuges for benthic invertebrates like the hyporheic zones and remnant pools is influenced by the severity and duration of the dry phase, as these factors constrain the presence of water (Lake, 2011). Survival in dry sediments as desiccation-tolerant life stages is also influenced by the harshness of drying (Stubbington & Datry, 2013). For instance, droughts intensify the severity, duration, and spatial extent of drying in IRES, causing streams to contract into isolated pools or dry out completely for extended periods (Lake, 2011). During a drought, the distances between pools, pool sizes, and the extent of desiccation of the sediment and litter all

increase when compared to the normal years (Sarremejane et al., 2022). Additionally, perennial springs and hyporheic zone are significantly affected by declines in the groundwater table, modifying the invertebrate assemblages in the wet refuges and their ability to recolonise the entire stream network upon flow resumption (Bogan & Lytle, 2011).

Effects of drying on OM decomposition

Results from Chapter 3 highlight the substantial variability in OM decomposition across the stream network throughout a hydrological year, which is attributable to the transition from aquatic to terrestrial habitats due to drying. Notably, as expected, the OM decomposition rate decreases with an increasing cumulative duration of flow interruptions (total number of non-flow days). OM tends to degrade faster in aquatic environments than in terrestrial ones (Mora-Gómez et al., 2020). For instance, in an ephemeral stream of the Algars stream network (E11, Figure I3.1), OM decomposition occurs exclusively under terrestrial conditions. Furthermore, it was noted that the stream reaches experiencing over 170 non-flow days (A8 & E15) demonstrated OM decomposition rates akin to those in E11, with up to an 8-fold reduction in the OM processed when compared to the perennial reaches (Chapter 3). However, this could have been influenced by the specific location within the stream network and local environmental conditions.

At the stream network scale, the flow regime exerts a strong influence on OM dynamics, affecting the processing, accumulation and downstream transport of OM (von Schiller et al., 2017). This results in a spatial heterogeneity in the distribution of OM and its chemical diversification (Del Campo et al., 2021). For instance, OM tends to accumulate on streambeds during the dry phase (Datry, Foulquier, et al., 2018), whereas OM is processed during wet phases (Abril et al., 2016). Upon flow resumption, OM is mobilised and transported downstream, potentially accelerating its decomposition in downstream reaches under flowing conditions (del Campo et al., 2021). This pulsed processing of OM, characterised by cycles of accumulation, transport, and decomposition, impacts resource availability for aquatic communities across the stream network (Larned et al., 2010; Datry et al., 2018), particularly influencing food webs and possibly resulting in dietary shifts in the invertebrate

community (Rosi-Marshall & Wallace, 2002). For instance, in the Algars stream network, the relative species richness of shredder aquatic invertebrates, which feed on particulate OM (> 1 mm), is higher during the autumn and winter. This increase aligns with the leaf-fall season and the subsequent resumption of flow after the summer, which aids in the downstream transport of OM. The relative richness of grazers, which consume biofilms composed of microbes, algae, and detrital OM, is higher in the winter than in summer (the dry season) and, favoured by flowing conditions. Conversely, filter feeders exhibit a tendency to increase during the summer, likely due to the predominance of detritus as the main source of OM available prior to the dry phase (López-Rodríguez et al., 2012). However, the abundance of predators is at its lowest in the autumn, coinciding with the reconnection of flow and the beginning of invertebrate recolonisation (Chapter 1). These seasonal patterns respond to the flow regime of Mediterranean intermittent streams and the availability of food resources (Álvarez & Pardo, 2009; López-Rodríguez et al., 2012; Muñoz, 2003). Interestingly, in the Algars stream network, no feeding group demonstrates a correlation with OM decomposition rates.

The OM decomposition rates in Chapter 3 were calculated using standardised wooden tongue depressors, which decompose primarily through microbial activity (Arroita et al., 2012). In addition, wood is less susceptible to physical abrasion than leaves and integrates the impact of environmental conditions in the stream over a period ranging from one to several months. This approach yields more reliable results than short-term measurements, which tend to be highly variable (Collier, 2014). Specifically, a strong correlation between decomposition rates and fungal biomass underscores the dominant role of aquatic fungi in OM decomposition in the Algars stream network (Chapter 3). Aquatic fungi, recognised as the primary drivers of OM decomposition in streams, facilitate decomposition both through direct litter consumption and by enabling its consumption by invertebrates (Graça, 2001). The response of fungi to flow variability may shed light on the differences in OM processing in the Algars stream network. For example, the cumulative duration of flow interruptions exerts more influence on OM decomposition than the frequency of these interruptions (Chapter 3). Although aquatic fungi are adversely affected by drying, their recovery is typically rapid, attributable to their short life cycles and adaptations to

flowing waters such as their conidium shape (Kuehn, 2016). In the Algars, the fungal biomass was observed to increase over time, suggesting rapid fungal recuperation and activity following flow resumption. Additionally, aquatic fungi exhibit less vulnerability to drying than bacteria (Duarte et al., 2017). In intermittent stream networks, aquatic fungi display different degrees of tolerance to drying, the main abiotic factor influencing their composition in such watercourses (Arias-Real et al., 2023). Other factors, including water nutrient enrichment and light exposure, can also modulate microbial communities and ecosystem functioning such as OM decomposition.

Impacts of drying and land use on invertebrate diversity and organic matter decomposition in an intermittent stream network

As previously discussed, aquatic diversity and OM decomposition in intermittent natural stream networks are impacted by drying (Chapter 3). Additionally, these systems face pressures similar to those in other freshwater systems, predominantly of an anthropogenic origin. Agriculture, one of the most widespread activities transforming the landscape, exerts both direct and indirect perturbations on stream ecosystems, such as nutrient enrichment, morphological channel alterations, and riparian vegetation removal (see references in Chapters 1 and 3). Water nutrient enrichment is recognised as a significant predictor of ecological degradation in European rivers (Grizzetti et al., 2017). Excessive nutrients lead to profound changes in aquatic diversity and ecosystem functioning (Woodward et al., 2012).

Despite extensive literature documenting the individual effects of drying or agricultural impacts on aquatic invertebrate diversity and OM decomposition (see references in Chapters 1 and 3), the potential accumulative effects of both stressors acting together on an entire natural intermittent stream network during a hydrological year are not understood well. This gap arises primarily from the difficulties in studying entire stream networks and the relatively little information on the effects of multiple factors in ecological studies. Understanding the effects of multiple stressors on ecosystem responses is crucial for anticipating how freshwater ecosystems will react

to global change. This importance is heightened due to the expected increases in both the temporal and spatial extent of drying. Such drying exacerbates the impact of rising human pressures, including water demand and pollution, consequently elevating the concentrations of nutrients and pollutants originating from human activities.

Effects of land use practices on aquatic diversity

Chapter 1 details how agricultural and natural land use practices in the Algars catchment affect invertebrate diversity. In particular, the concentration of dissolved inorganic nitrogen (DIN), largely derived from the nitrates used in agricultural activities, and the river habitat index (IHF, from *Índice de Hábitat Fluvial*), an indicator of areas less impacted by human activities, have been found to influence both taxonomic and functional diversity. The beneficial role of habitat heterogeneity in diversity is a fundamental concept in ecology (Macarthur, 1965; Stein et al., 2014). In the Algars catchment, the IHF strongly correlates with the natural land cover (Spearman's correlation coefficient, 0.64) and canopy cover (Spearman's correlation coefficient, 0.87). The catchment is predominantly characterised by naturalised coniferous forests, accounting for 32% of the total land cover, and bushy sclerophyllous vegetation, covering 9% predominantly in the headwater subcatchments. The limited penetration of sunlight affects primary production, rendering allochthonous litter a crucial component of the aquatic food webs (Vannote et al., 1980). Vegetation not only provides essential OM to food webs, but also acts as a buffer, protecting the aquatic ecosystem from extreme temperature fluctuations during drying (Dan Moore et al., 2005) and reducing evaporation in the summer (Biederman et al., 2014). Moreover, during dry phases, the canopy offers protection against rain, solar radiation, and heat, all of which are abiotic factors influencing the decomposition process (see section below; Del Campo et al., 2019).

The IHF positively affects taxonomic α-diversity, functional richness, and redundancy (Chapter 1). An increase in habitat heterogeneity supports not only a rise in sensitive taxa (EPT) and their functions due to more suitable habitats, but it also increases the number of species fulfilling similar ecological roles (functional redundancy, FRed). The aquatic communities of natural intermittent streams show high functional redundancy, which can increase at the beginning of drying. However,

functional redundancy cannot compensate for the loss in diversity in response to increased drying (Chapter 1;Crabot, Mondy, et al., 2021). As the redundancy concept suggests that functionally similar taxa might compensate for the loss of others, functional redundancy ensures that a community efficiently and stably performs its functions over time (Bruno et al., 2016; Rosenfeld, 2002). Therefore, in a scenario of increasing drying, the preservation of aquatic communities could be linked to an increase in their functional redundancy. This can be achievable by prioritising the conservation of habitat heterogeneity and natural areas.

Agricultural practices have both direct and indirect negative impacts on freshwater systems, as extensively documented (see references in Chapters 1 and 3). Over-enrichment with nutrients, predominantly nitrogen and phosphorus, can lead to eutrophication, eroding diversity and disrupting trophic interactions (van der Lee et al., 2021; Wang et al., 2021). However, contrary to one of my hypotheses, nutrient enrichment increased taxonomic diversity and functional richness in the Algars (Chapter 1). As outlined in Chapter 1, moderate nutrient enrichment might initially benefit aquatic diversity until it reaches detrimental levels (subsidy-stress effect, Niyogi et al., 2007; Odum et al., 1979). For instance, in the downstream sections of the Algars, where agricultural practices constitute over 50% of land use, the permanent reaches (A4 and A5) exhibited higher taxonomic and functional richness than the intermittent reaches (from A6 to A9), but not greater levels of sensitive taxa (EPT) and functional redundancy (Chapter 1). Nutrient enrichment in water enhances microbial activity and litter quality, leading to changes in food availability that, at moderate levels, can increase the abundance and biomass of invertebrates, especially grazers and detritivores (Gulis et al., 2006; Lawrence & Gresens, 2004). Specifically, generalist taxa often thrive in nutrient-rich ecosystems, resulting in the exclusion of specialists (Gafner & Robinson, 2007). However, escalating stress levels can lead to a decline in both taxonomic and functional richness (Voß & Schäfer, 2017).

In Chapter 1, drying was identified as the sole factor impacting temporal β-diversity, partially aligning with my initial hypotheses. Flow regime is the main driver of aquatic diversity in the Algars stream network. However, previous studies indicate that agricultural activities can contribute to a reduction in β-diversity, driven by community homogenisation through the loss of sensitive taxa as well as diminished heterogeneity

and quality of the habitats (Cook et al., 2018; Hill et al., 2016; Sueyoshi et al., 2016). For instance, in the Algars, the IHF in the streambed correlates highly with the canopy cover and land use practices (0.87 and 0.64, respectively), decreasing with agricultural practices in the catchment (Chapter 1). Drying can exacerbate the impacts of agricultural practices, such as certain physicochemical changes related to flowing conditions, particularly in open-canopy areas (Gómez et al., 2017). In such areas and in isolated pools, reduced flow can result in higher water temperatures. Furthermore, evaporation might cause evapoconcentration, leading to a higher concentration of solutes, notably in reduced forms like ammonium, which can be particularly toxic to the sensitive taxa (Camargo & Alonso, 2006; Siebers et al., 2020; Von Schiller et al., 2011). The rise in nutrient concentration and other pollutants notably from agricultural sources, such as pesticides and fine sediment, poses a significant threat to invertebrate diversity, with a particularly detrimental impact on the sensitive taxa (Piggott et al., 2012; Stubbington, Bogan, et al., 2017). Nevertheless, the consequences of drying are more pronounced in regions with intensive agricultural activities compared to those with natural vegetation. In summary, land use changes in the IRES catchment resulting from anthropogenic activities significantly affect invertebrate diversity, thereby intensifying the adverse effects of drying.

Effects of land use practices on OM decomposition

Changes in land use in intermittent stream networks also significantly impact ecosystem functions. As highlighted in Chapter 3, a positive correlation exists between OM decomposition rates, fungal biomass, and DIN concentration, which is typically associated with agricultural activities. One of my hypotheses posited that the presence of nutrients in stream water could mitigate the adverse effects of drying, thereby enhancing decay rates under flowing conditions (Chapter 3). Indeed, the permanent reaches with the highest water DIN concentrations in the Algars (A4 and A5; Figure I.5) exhibit the highest OM decomposition rates and fungal biomass, up to twice that found in the non-agricultural permanent reaches (Chapter 3). Moderate nutrient enrichment is shown to positively influence these rates (Pascoal et al., 2021). Specifically, nutrient enrichment stimulates the decomposition of OM, particularly the less nutritious substrates like wood, primarily through microbial communities that are more nutrient-

limited (Díez et al., 2002; Gulis et al., 2004). However, excessive nutrient concentrations can negatively impact OM decomposition, as observed in highly eutrophic streams where levels of ammonium or other compounds may become toxic to the aquatic decomposers, particularly invertebrates and fungi (Baldy et al., 2007; Camargo & Alonso, 2006; Duarte et al., 2009; Lecerf et al., 2006). Therefore, the impact of agricultural nutrients on OM decomposition can display a hump-shaped relationship with increasing levels of water nutrient enrichment (Woodward et al., 2012). Yet, responses to increased nutrient enrichment may vary among different microbial decomposer groups. Although fungal biomass increases at moderate nutrient levels and decreases under hypertrophic conditions (Duarte et al., 2009; Dunck et al., 2015), bacterial biomass demonstrates a linear increase (Pascoal et al., 2021). Nevertheless, a strong correlation ($R^2 = 0.70$; Chapter 3) between OM decomposition rates and fungal biomass in the Algars underscores the key role of aquatic fungi in this process (Chapter 3).

The adverse effects of drying in the Algars are not fully offset by water nutrient enrichment. For instance, the agricultural section with the longest cumulative duration of flow interruptions (A8; Figure I.5) exhibits the lowest decomposition rates and fungal biomass that are comparable to the rates found in terrestrial environments. Additionally, the flow regime significantly influences the physical and chemical properties of the water in streams, subsequently affecting microbial decomposer metabolism (Pascoal et al., 2021). For instance, in isolated pools exposed to solar radiation, water temperature and OM accumulation can increase, while oxygen levels may decrease (Canhoto et al., 2013; Von Schiller et al., 2011). In such low-oxygen environments, fungal biomass decreases (Abril et al., 2016; Canhoto et al., 2013). Microbial activity tends to decline during drying, significantly dropping in the emerged OM during dry phases (Chapter 3; Mora-Gómez et al., 2018). Nonetheless, aquatic decomposition can persist in wet refuges like subsurface sediments or remnant pools during dry phases (Abril et al., 2016; Arias-Real et al., 2020). Agriculture introduces additional stressors, such as sedimentation and agrochemicals, further reducing OM decomposition (Voß et al., 2015).

Other agricultural impacts on stream functioning include channel modification, water pollution, and riparian vegetation removal (Kominoski et al., 2021). In the Algars,

canopy cover positively correlates with OM decomposition rates and fungal biomass (Chapter 3). Canopy cover strongly correlates with the percentage of natural land cover (Spearman's correlation coefficient, 0.60; data from Chapters 1 and 3), predominantly in the headwaters composed mainly of coniferous forests. In forested streams, allochthonous plant litter is a crucial resource for aquatic food webs, with fungi playing a key role in OM decomposition (see references in Chapter 3). Canopies reduce the incidence of sunlight, favouring fungi, which outcompete algae for inorganic nutrients (Danger et al., 2013). In the Algars, canopy cover mitigates the negative effects of drying on OM decomposition, although to a lesser extent than DIN enrichment from agriculture (Chapter 3). Furthermore, canopy cover correlates with habitat heterogeneity in the streambed (IHF; Spearman's correlation coefficient, 0.85; data from Chapters 1 and 3), which positively correlates with invertebrate diversity. Invertebrates, processing the plant litter conditioned by aquatic fungi, play an important role in OM decomposition in streams (Jonsson & Sponseller, 2021). However, the relative importance of invertebrates and microbes in OM decomposition varies seasonally and longitudinally (Graça et al., 2001). Invertebrates might play a more significant role than microbes in forested streams, with the opposite true in agricultural streams (Hladyz et al., 2010). However, in the Algars, shredder abundance and richness do not vary significantly with the position in the network, agricultural parameters, or decomposition rates, suggesting that the current levels of agriculture in the network do not adversely affect this trophic group (data from Chapters 1 and 3). This observation may be attributed to the fact that moderate levels of agriculture can enhance shredder richness and density (Hagen et al., 2006).

Land use influences decomposition processes across the entire stream network, but this effect is contingent upon local conditions and network position. In the Algars, forested headwaters with low nutrient contents contrast starkly with the downstream agricultural areas with higher nutrient enrichment (Figures I.5 and 3.4). Forested headwaters provide more stable OM decomposition conditions than the downstream agricultural areas, as indicated by the lower seasonal variation in the physical and chemical parameters such as nitrate concentration (Chapter 1; Abril et al., 2015). Although OM decomposition rates increase with nutrient enrichment or high canopy cover, these factors are not enough to counteract the effects of prolonged dry phases.

Chapter 3 reveals that the stream reaches experiencing more than 170 days without flow exhibit decomposition rates similar to those of terrestrial environments. However, local factors and processes also significantly influence OM decomposition, potentially altering this threshold. For instance, sediment grain size and type are critical in determining the presence of wet refuges that enable the continuation of aquatic OM decomposition (Arias-Real et al., 2020). In these habitats, aquatic organisms, including microbes and invertebrates, can survive *in situ* during dry phases, maintaining some level of activity in refuges such as hyporheic zones (Chapter 2; Arias-Real et al., 2020). This complex interplay between land use, environmental factors, and aquatic biodiversity underscores the need for comprehensive ecosystem management strategies. In the Algars, and similar intermittent stream networks, mitigating the negative impacts of drying while preserving natural stream functions is crucial.

Global Change, limitations, and future research

Global change: implications for IRES

There has been a paradigm shift in limnology in recent decades, characterised by an increasing research interest in IRES, which represent nearly 50% of global watercourses (Messager et al., 2021). Intermittent segments are more prevalent than perennial ones across all river networks (Datry et al., 2023). Despite the extensive literature on IRES ecosystems, these systems are experiencing spatial and temporal expansion due to human-induced climate change (Datry et al., 2016, 2023; Datry, Larned, & Tockner, 2014; Larned et al., 2010). For instance, changes in atmospheric vapour content induced by human activities in Europe, especially in the Mediterranean region, have increased the risk of wildfires and extreme drought events (Treydte et al., 2023). Additionally, the persistent anticyclonic anomaly observed over Western Europe in 2022, potentially a 'thermodynamic' effect of global warming, has exacerbated exceptional drought conditions that continue to persist (Faranda et al., 2023). The increasing frequency and intensity of climate extremes, such as droughts and floods, are expected to profoundly impact the flow regimes of watercourses (Schneider et al., 2013). Although IRES face similar anthropogenic threats as perennial watercourses,

they are arguably under a greater threat of degradation due to less legal protection and a lower social value (Chiu et al., 2017).

The spatiotemporal expansion of IRES is also directly linked to human activities requiring water, such as intensified agriculture and urbanisation. In the Ebro Basin, where the Algars stream network is located, human water demand has risen by 57% in the last 40 years and is projected to increase by a further 38% to 58% by 2050 (Grouillet et al., 2015). The combination of climate change and an increased water demand may intensify drying in natural IRES and transform many watercourses from perennial to intermittent flow regimes (Costigan et al., 2017). In the Algars, traditional rain-fed agriculture, including crops like olive trees, almond trees, and vineyards, has been predominant (Chapters 1 and 3). However, recent decades have seen a transformation towards irrigated agriculture, shifting to crops like peach, cherry, and apple trees (Pellicer, 2013). This transition from rain-fed to irrigated agriculture not only alters the flow regime, but also increases nutrient loads in the water (Oduor et al., 2023).

Conversely, flow regulation and water addition in IRES can transform intermittent streams or sections into perennial ones, a process known as 'perennialization' (Chiu et al., 2017). While perennialization is often associated with benefits such as an improved water quality and enhanced habitats for aquatic and riparian biota (Brooks et al., 2006), it can have detrimental effects if sustained by effluent discharge, leading to water pollution that is harmful to aquatic communities (Mor et al., 2019; Skoulikidis et al., 2017). Perennialization may also lead to the local extinction of IRES-specialist biota, homogenising and reducing certain groups such as the pool-specialist Coleoptera taxa (Stubbington, Bogan, et al., 2017). In the Algars, an increase in temporal β-diversity with drying suggests greater heterogeneity in the assemblages from the intermittent reaches than the perennial ones over time (Chapter 2). However, the ecological consequences of perennialization remain unclear.

Human activities are transforming the landscape. Changes in land use, particularly the intensification of agriculture and urbanisation, are exerting both direct and indirect perturbations in stream ecosystems. These include nutrient enrichment, morphological channel alterations, changes in surface runoff, and riparian vegetation removal (Kominoski et al., 2021). Agriculture intensification and wastewater treatment

can increase the levels of water nutrients and pollutants, such as pharmaceuticals and pesticides. During drying periods, the concentration of these compounds may increase and their effects may be amplified in combination with those of drought events (Sarremejane et al., 2022). For instance, in the Guadiana Basin, the highest concentrations of different pharmaceuticals that are highly toxic to aquatic life have been found during the dry phases in drought years and after heavy rainfalls following the resuspension of substances from the sediments (Palma et al., 2020). Although moderate nutrient enrichment in the Algars confers benefits for decay rates and some diversity metrics (Chapter 1 and 3), an increase in drying intensity can lead to nutrient accumulation during dry phases, severely impacting the quality of stream water upon flow resumption and affecting both diversity and ecosystem functioning (Arce et al., 2014).

Global change, including the impact of climate change and human pressures, is affecting IRES communities. The spatial and temporal expansion of IRES, coupled with the increasing frequency and intensity of drought events, can affect the distribution and composition of species assemblages, as well as compromise the strategies to survive drying (Datry, Boulton, et al., 2018; Sarremejane et al., 2021). For instance, the use of wet refuges during dry periods by aquatic invertebrates and their survival as part of invertebrate seedbanks are contingent on the severity of drying and water availability (Chapter 2; Stubbington & Datry, 2013). However, the extent to which biota can adapt to these disturbances greatly depends on the predictability of such events (Lytle et al., 2007). Therefore, prolonged dry phases might exceed the endurance threshold of the adapted organisms in wet refuges or invertebrate seedbanks, potentially leading to mass mortality events (Aspin, Hart, et al., 2019). Furthermore, recolonisation efforts may be jeopardised by increased spatial and temporal fragmentation, particularly in isolated sections such as many headwaters (Gauthier et al., 2020). Specifically, the connectivity and proximity of a community to perennial refuges are crucial for community recovery upon flow resumption (Bogan et al., 2015; Jaeger et al., 2014; Sarremejane et al., 2020). The extension of drying can transform perennial refuges into intermittent habitats, adversely affecting strictly aquatic organisms. Therefore, changes in IRES flow regimes, particularly the extension of dry phases, could drastically disrupt communities adapted to predictable drying regimes, potentially

leading to long-term and irreversible shifts in population dynamics and community composition. This would limit the effectiveness of rescue effects after a disturbance (Bogan & Lytle, 2011; Crabot et al., 2020; Jaeger et al., 2014; Sarremejane et al., 2021).

Changes in IRES flow regimes can also affect ecosystem functioning such as OM decomposition. The intensification of drying can modify the total amount of OM processed in stream networks and affect OM quality (Granados et al., 2022; von Schiller et al., 2015; Ylla et al., 2010). Specifically, aquatic OM processing ceases during dry phases, leading to accumulation on dry streambeds (Del Campo et al., 2021). In the Algars, decay rates resembling terrestrial OM decomposition rates were observed in the reaches experiencing 170 days of non-flow conditions within a hydrological year (Chapter 3). A spatiotemporal increase in drying can result in a reduction of the OM processed in the stream network. However, upon flow resumption, not only is aquatic decomposition reactivated, but there is also a downstream transport of OM. Sudden floods can cause physical abrasion and massive downstream transport, while gradual rewetting favours the initiation of microbial decomposition over transport (Del Campo et al., 2021). The increase in OM accumulation and its downstream transport can mobilise large quantities of nutrients and other compounds, potentially leading to enhanced microbial activation or toxic effects due to a resuspension of certain pollutants (Dunck et al., 2015). Aquatic invertebrates, being highly sensitive to drying, take longer to recover after flow resumption (Datry, Foulquier, et al., 2018). By contrast, aquatic fungi rapidly recover with flow resumption. However, fungi are more sensitive to changes in water quality than bacteria, displaying a unimodal response to nutrient loads, whereas bacterial biomass benefits from nutrient loads and show a linear response (Duarte et al., 2009; Pascoal et al., 2021). Therefore, with an intensification of drying, IRES communities, particularly in disturbed catchments such as agricultural areas, could undergo significant changes, affecting the processing and transport of OM throughout the stream network.

In summary, in the Algars stream network, high canopy cover and habitat heterogeneity positively correlate with diversity metrics and OM processing (Chapters 1 and 3). These variables are strongly associated with natural land uses in the Algars catchment, particularly in the headwaters, highlighting the critical need to preserve these areas to mitigate the effects of drying. Headwater systems play a vital role in

nutrient dynamics and provide habitats for aquatic biota, thus supporting a significant portion of catchment biodiversity (Meyer & Wallace, 2001). Specifically, the Algars headwaters, situated in a protected mountain area with a maximum altitude of 1339 m.a.s.l., are instrumental in facilitating the downstream dispersion and transport of water and nutrients upon flow resumption. Despite the presence of drying sections throughout the stream network, the conservation of natural headwater areas in Mediterranean streams, along with the maintenance of sustainable water discharges to preserve perennial and wet refuges, are key in supporting IRES communities. These measures are increasingly vital in the face of the expanding spatiotemporal extent of IRES, driven by global climate change and human activities. Effective management and conservation strategies in these areas are essential for maintaining ecological integrity and resilience, ensuring the continued support of the rich biodiversity and services these ecosystems provide.

Limitations and future research

The growing research interest in IRES marks a significant advancement in our understanding and management of these systems. This interest is increasing globally and includes historically underrepresented areas in the Global South (Cambray, 1991; Chakona et al., 2008; Mao, 2023; Rocha et al., 2012). However, there are still substantial gaps in our understanding of IRES networks, particularly in the context of the intensification of extreme events.

Mapping of IRES drying including temporal and spatial variability

One major challenge in understanding the impact of drying on biodiversity and ecosystem functions at the network scale lies in balancing data resolution with economic cost and time investment. During the research performed for this thesis, the loss of several sensors and the associated costs to replace them increased the time investment needed to address the gaps in data. Although cheaper technologies exist for gathering real-time hydrological data that monitor the presence or absence of water and temperatures, future research should focus on developing technologies that can precisely track water level and discharge at a low cost and with minimal environmental impact. Increasing the density of monitoring points in a stream network will facilitate more comprehensive research, particularly in developing countries.

Studying network-scale dynamics over time is crucial for identifying 'hot spots' and 'hot moments' that influence biogeochemical cycles and biodiversity in IRES networks. This understanding is pivotal for managing and protecting these ecosystems in the face of climate change and water scarcity in order to preserve ecosystems and future water supply.

Additionally, mapping hydrological regimes across networks can assist managers in pinpointing the areas of concern, such as sources of pollution, illegal water abstraction for irrigation, and habitat fragmentation. Raising societal awareness of the ecosocial value of all watercourses and their role as common resources for current and future generations is also key in consolidating the protection of IRES ecosystems.

Improving the functional characterisation of IRES communities

Another challenge lies in enhancing the functional characterisation of aquatic communities. There is a need to expand knowledge on specific traits related to the resistance to drying. For example, the ability of some Coleoptera to survive within wet sediments during dry phases was not captured by the traits selected in Chapter 2. In addition, despite the extensive literature on invertebrate seedbanks, research is needed to improve our knowledge on the time or capacity to resist drying in the desiccation-tolerant life stages. Although a lot of research focuses on aquatic invertebrates, further studies are needed to understand the functional responses of other aquatic communities like fungi, particularly regarding their resistance to drying. Additionally, in this thesis, invertebrate identification was conducted at the genus level due to time and cost constraints. Advances in technology to reduce the cost of DNA assessment could improve the resolution of identification, enhancing functional characterisation by using trait datasets typically at the species level (Behrens-Chapuis et al., 2021; Duarte et al., 2021; Meyer et al., 2021). Moreover, expanding the DNA libraries of aquatic organisms is essential in improving these methods.

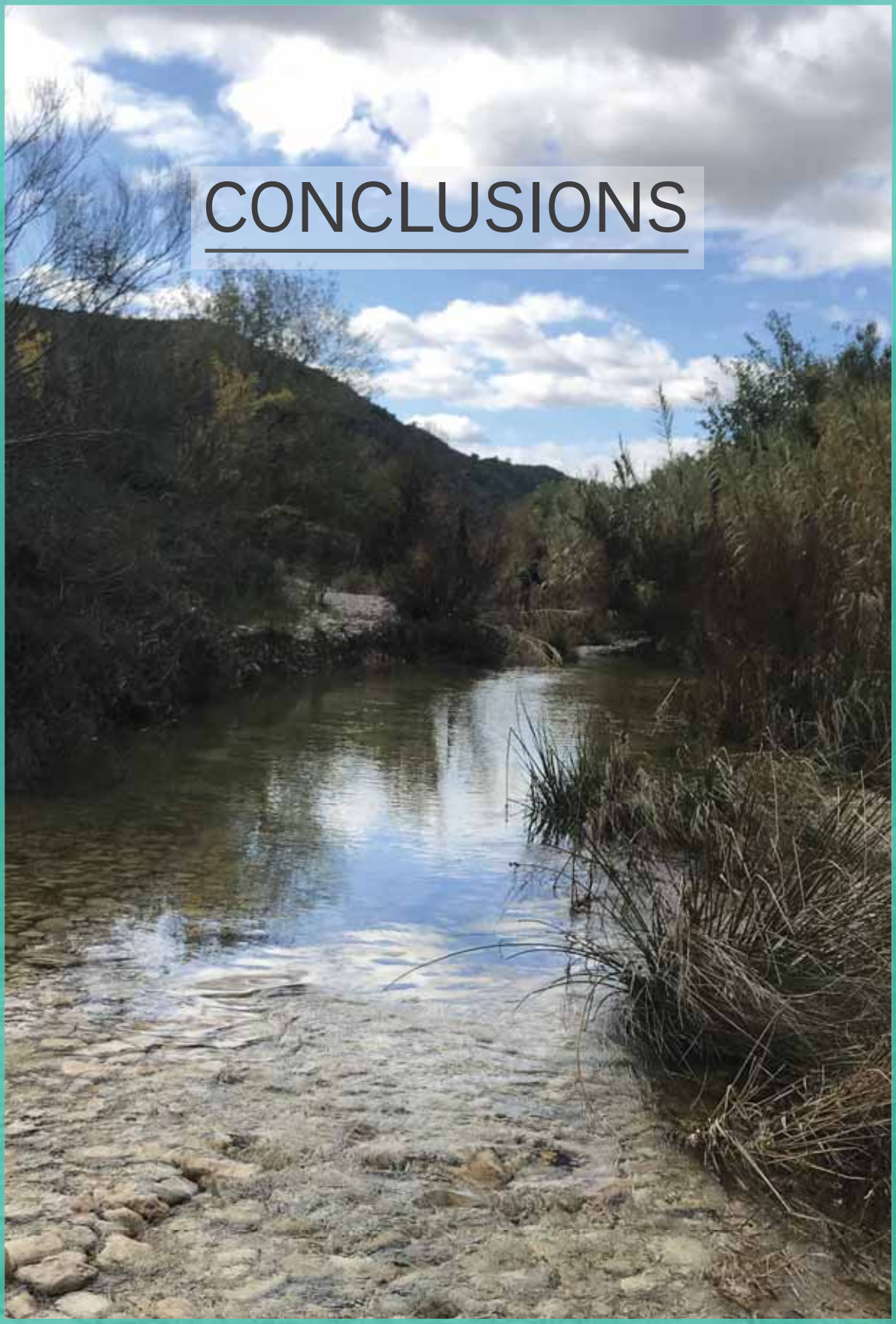
Exploring the role of refuges for IRES communities

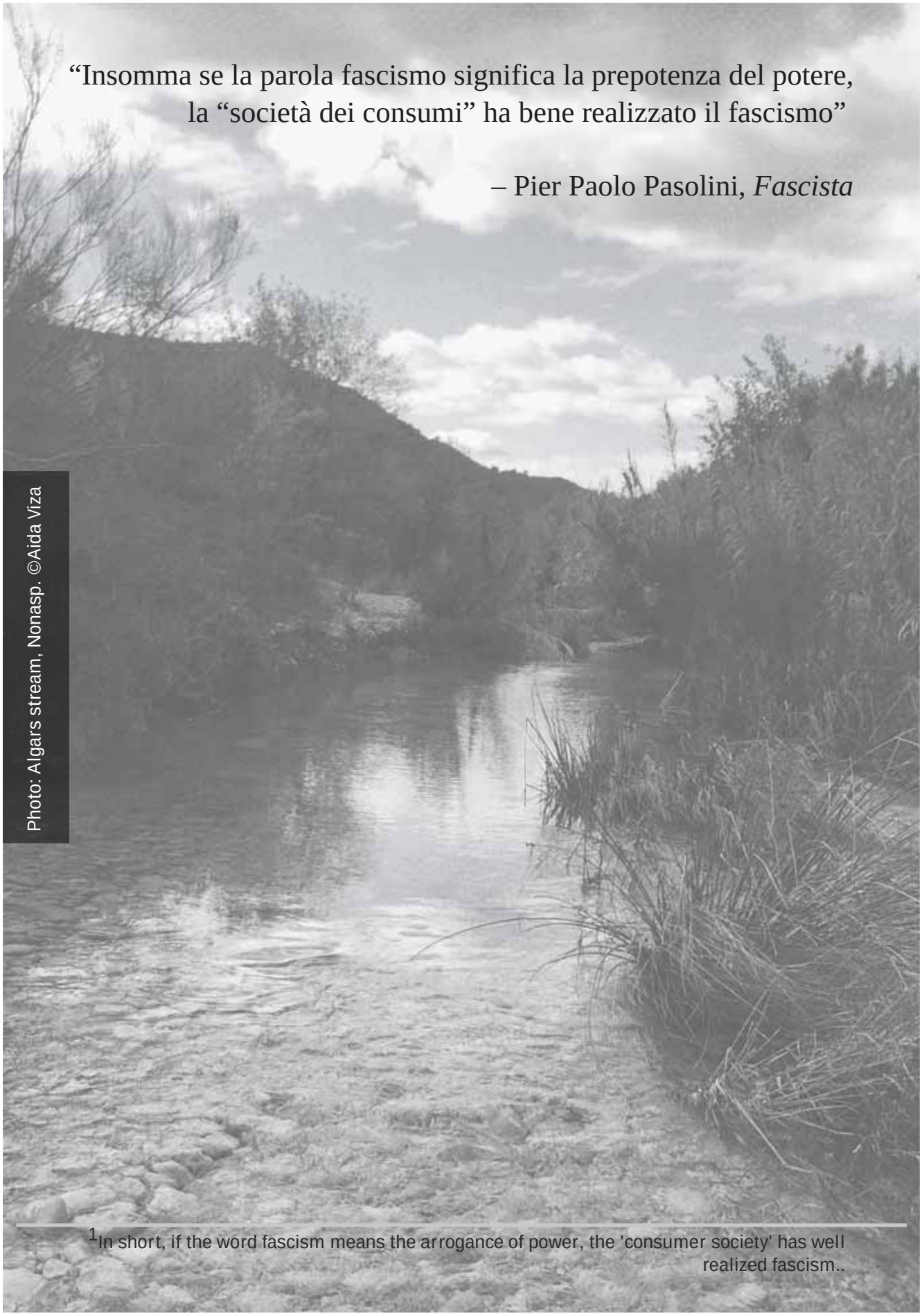
The increase in drought events and the associated expansion of drying in stream and river networks may threaten the adaptations of IRES communities to drying. The use of wet refuges during dry phases has been well-studied for aquatic invertebrates, but less so for organisms like aquatic fungi and bacteria. Given the crucial role of

microbes in OM processing, future studies should investigate their strategies for coping with drying. Although the original design of Chapter 2 included the study of fungal assemblages in rehydrated dry sediments, time constraints limited this exploration.

Understanding the thresholds of diversity and ecosystem functions in wet refuges under prolonged dry conditions can provide managers and researchers the predictive tools to better comprehend the stream community responses to drying in more arid scenarios. As mentioned before, future research should include the mapping of the network of wet refuges and their spatial and temporal dynamics to identify areas or sections with a greater capacity to maintain diversity and ecosystem functions during dry periods. This approach will aid in implementing protective measures for refuges in stream reaches, serving as sources for recolonisation and sustaining ecosystem functioning.

CONCLUSIONS





"Insomma se la parola fascismo significa la prepotenza del potere,
la "società dei consumi" ha bene realizzato il fascismo"

– Pier Paolo Pasolini, *Fascista*

Photo: Algars stream, Nonasp. ©Aida Viza

[1]In short, if the word fascism means the arrogance of power, the 'consumer society' has well realized fascism..

Conclusions

This thesis enhances our understanding of the impacts of drying and varied land use on biodiversity and ecosystem functioning in a Mediterranean stream network. It highlights the necessity of adopting a network-scale perspective, given the variability in drying across a network. Furthermore, it emphasises the critical importance of preserving potential refuges for aquatic diversity, especially in natural areas. The key findings from the three chapters of this thesis are summarised as follows:

Chapter 1: A comprehensive spatial analysis of invertebrate diversity in an intermittent stream network: responses to drying and land use

Drying varies across the stream network, negatively impacting α-diversity, positively influencing β-diversity, and acting as an environmental filter that increases nestedness.

Moderate nutrient enrichment from agricultural activities favours taxonomic α-diversity and functional richness, without significantly affecting β-diversity metrics.

High habitat heterogeneity in natural areas supports taxonomic and functional diversity, including the presence of sensitive taxa.

The results demonstrate that drying primarily dictates the taxonomic and functional composition of aquatic invertebrates, which exhibit a high level of adaptation to this natural disturbance. Direct impacts from agriculture were not evident, but natural areas offer more refuges to the specialist and sensitive taxa.

Chapter 2: The role of seedbanks and hyporheic refuges in supporting benthic invertebrate community resistance and resilience to dry phases

Aquatic invertebrate diversity in hyporheic and seedbank assemblages during dry phases constitutes a subset of the benthic assemblages during flow conditions, albeit with low representation.

Invertebrate assemblages in natural intermittent streams demonstrate a substantial abundance of traits related to the resistance and resilience to dry phases.

Extended dry phases may diminish resilience in hyporheic and seedbank assemblages.

This research is the first to compare the taxonomic and functional responses of hyporheic and seedbank assemblages during a dry phase to those of the benthic assemblages in flowing conditions.

Chapter 3: Contrary effects of flow intermittence and land uses on organic matter decomposition in a Mediterranean river basin

Extended dry phases negatively affect the OM decomposition process, slowing the rates to levels similar to those in terrestrial environments under severe desiccation.

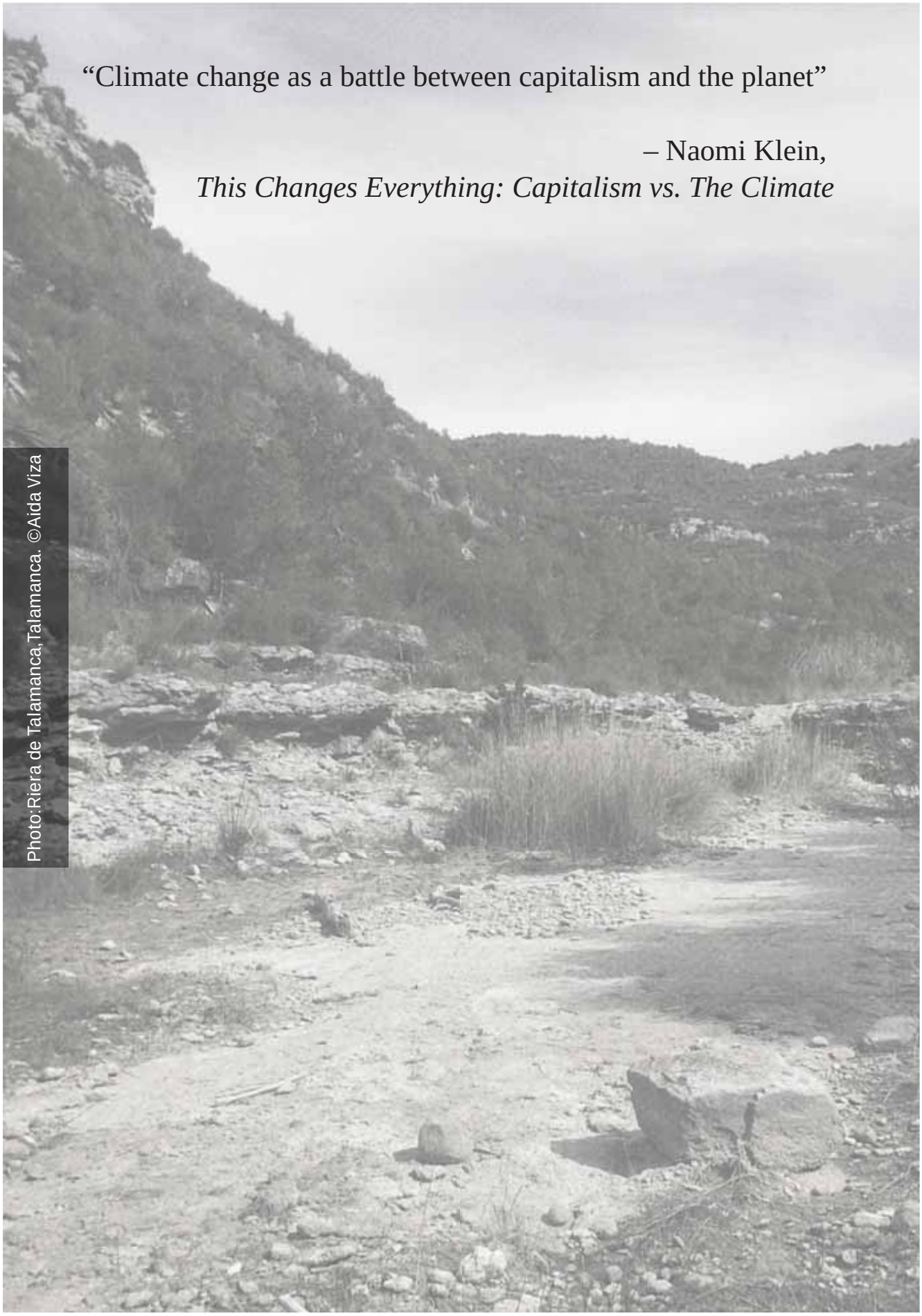
Drying interacts with other factors along the stream network, influencing OM processing. Water nutrient enrichment and canopy cover mitigate the adverse effects of drying, with the fastest decomposition rates observed in the permanent streams in agricultural areas.

The effects of high levels of drying cannot be offset by nutrient enrichment and canopy cover in the streambed. Reaches with over 170 days of drying exhibit decay rates comparable to terrestrial OM decomposition rates.

In small Mediterranean stream networks with varied land uses, aquatic fungi are the primary biotic agents driving OM decomposition. Canopy cover in headwater streams enhances fungal activity and may serve as a reservoir of diversity during dry periods for the entire stream network.

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"Climate change as a battle between capitalism and the planet"

– Naomi Klein,
This Changes Everything: Capitalism vs. The Climate

Photo:Riera de Talamanca,Talamanca. ©Aida Viza

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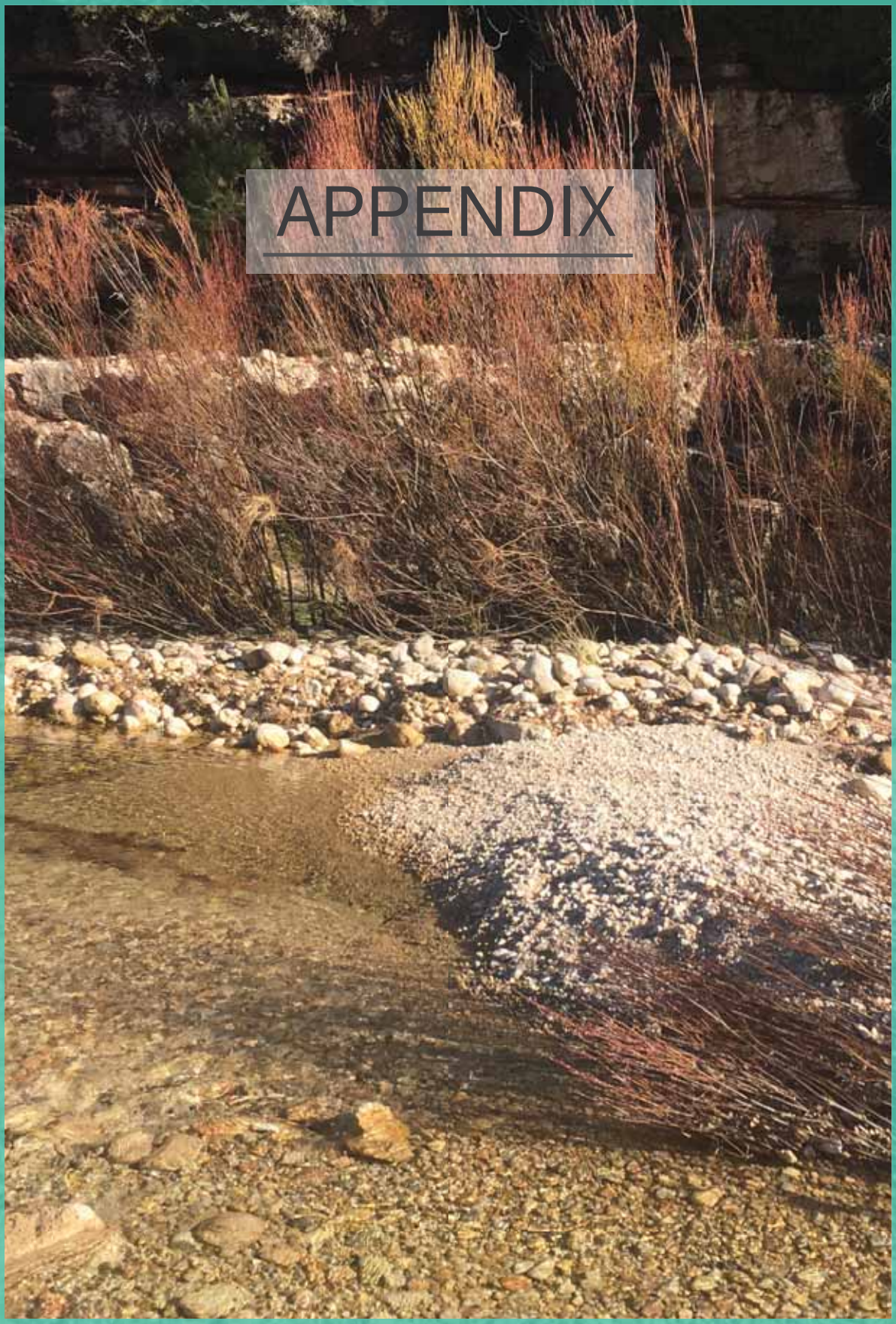
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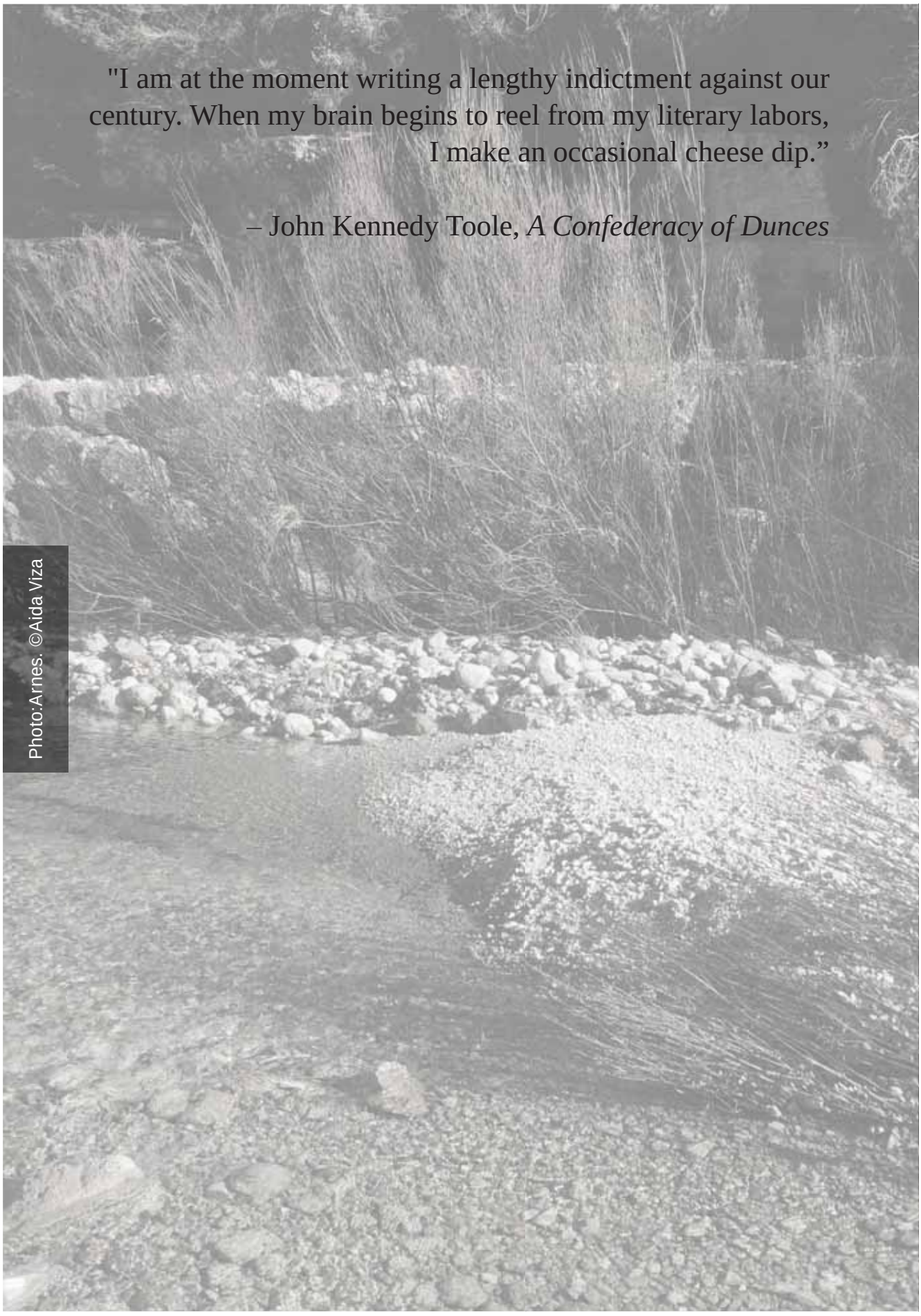
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APPENDIX





"I am at the moment writing a lengthy indictment against our century. When my brain begins to reel from my literary labors, I make an occasional cheese dip."

– John Kennedy Toole, *A Confederacy of Dunces*

Photo:Arnes. ©Aida Viza

Figure S1.1. Empirical variograms of: a) DIN, b) DD, c) TOC, d) Conduc-tivity, e) IHF.

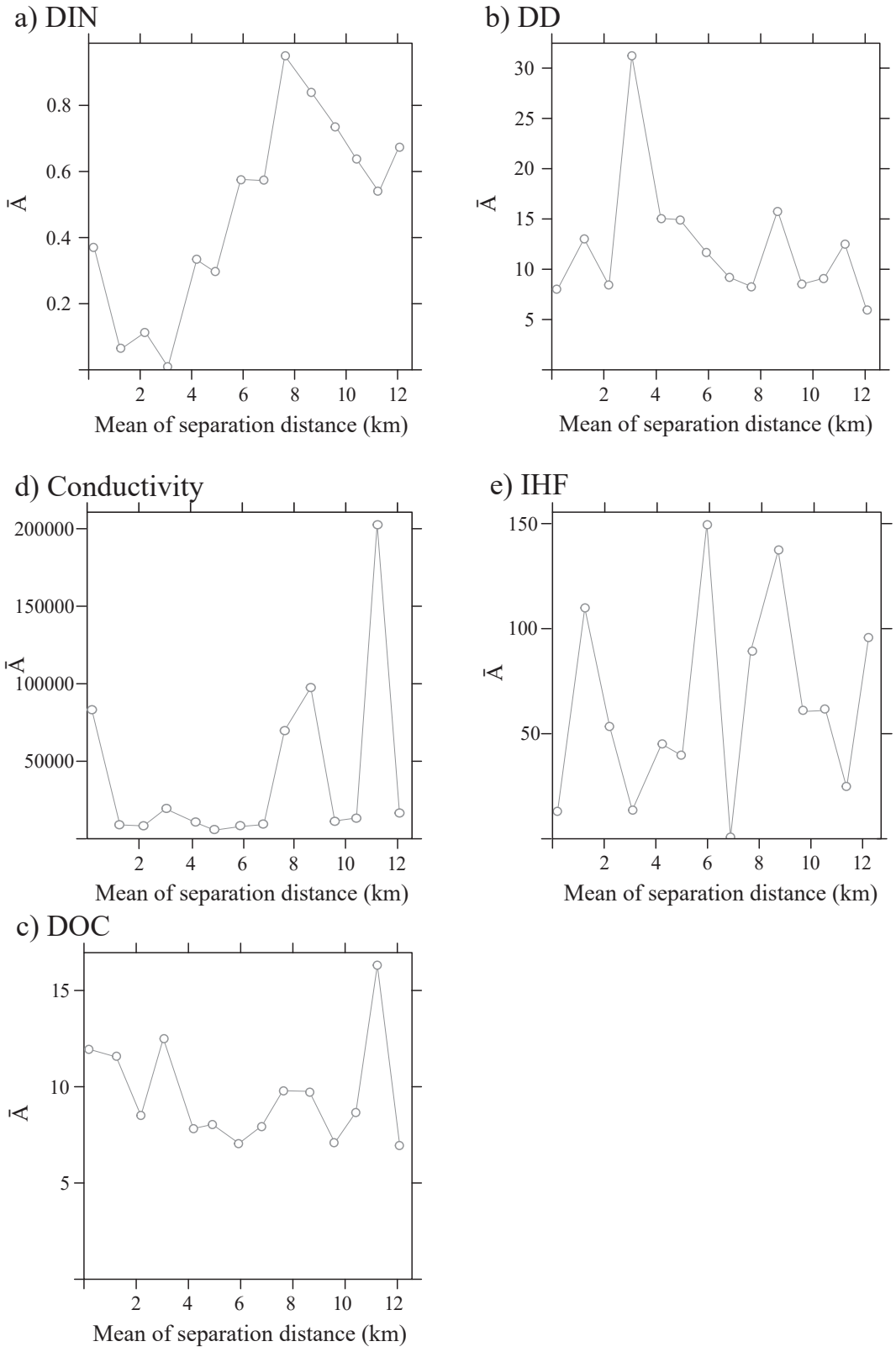


Figure S1.2. Plots of covariate coefficients and their confidence intervals (environmentally constrained gllvm model). Black crosses indicate significant coefficients. Taxa codes can be found in Table S4.

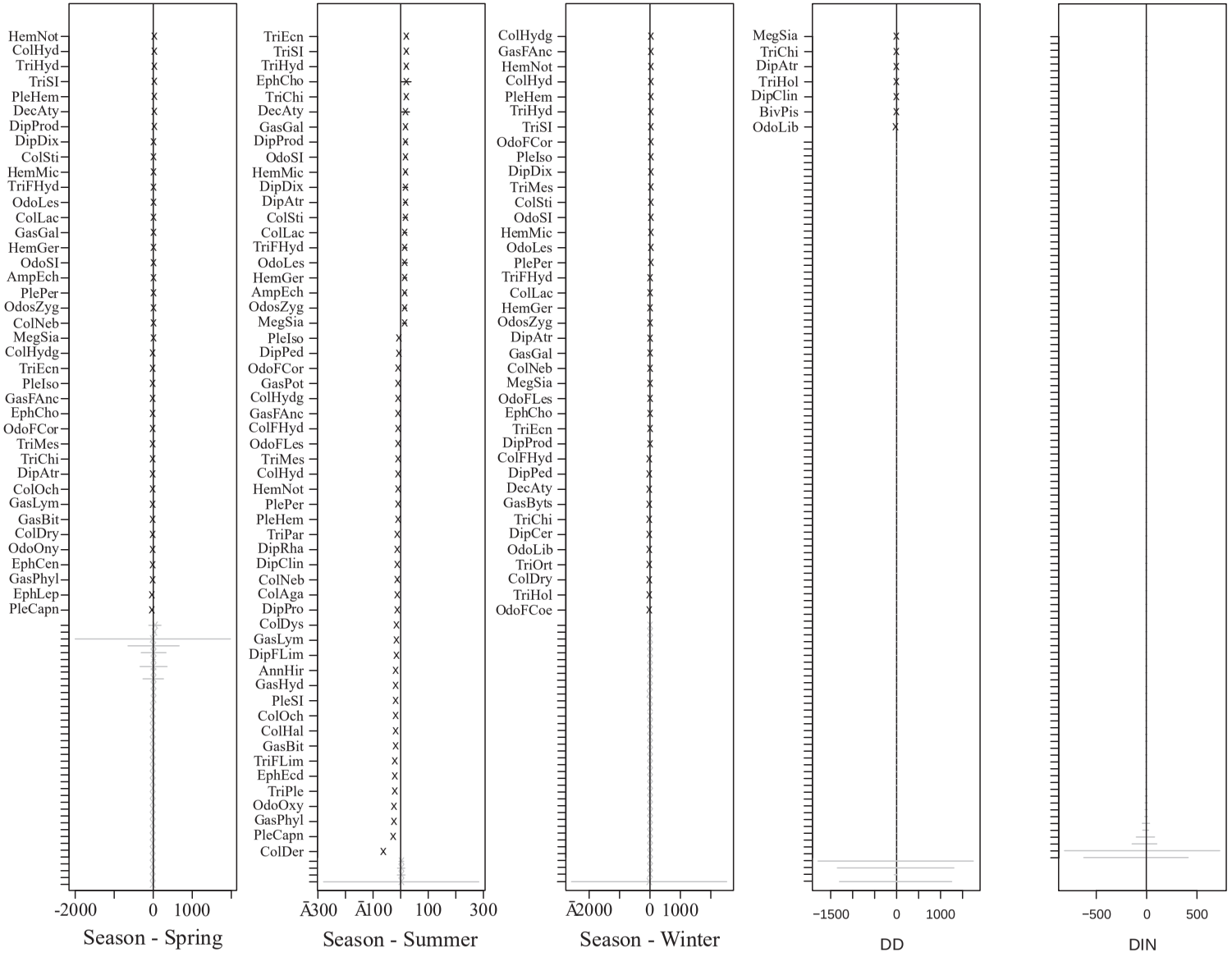
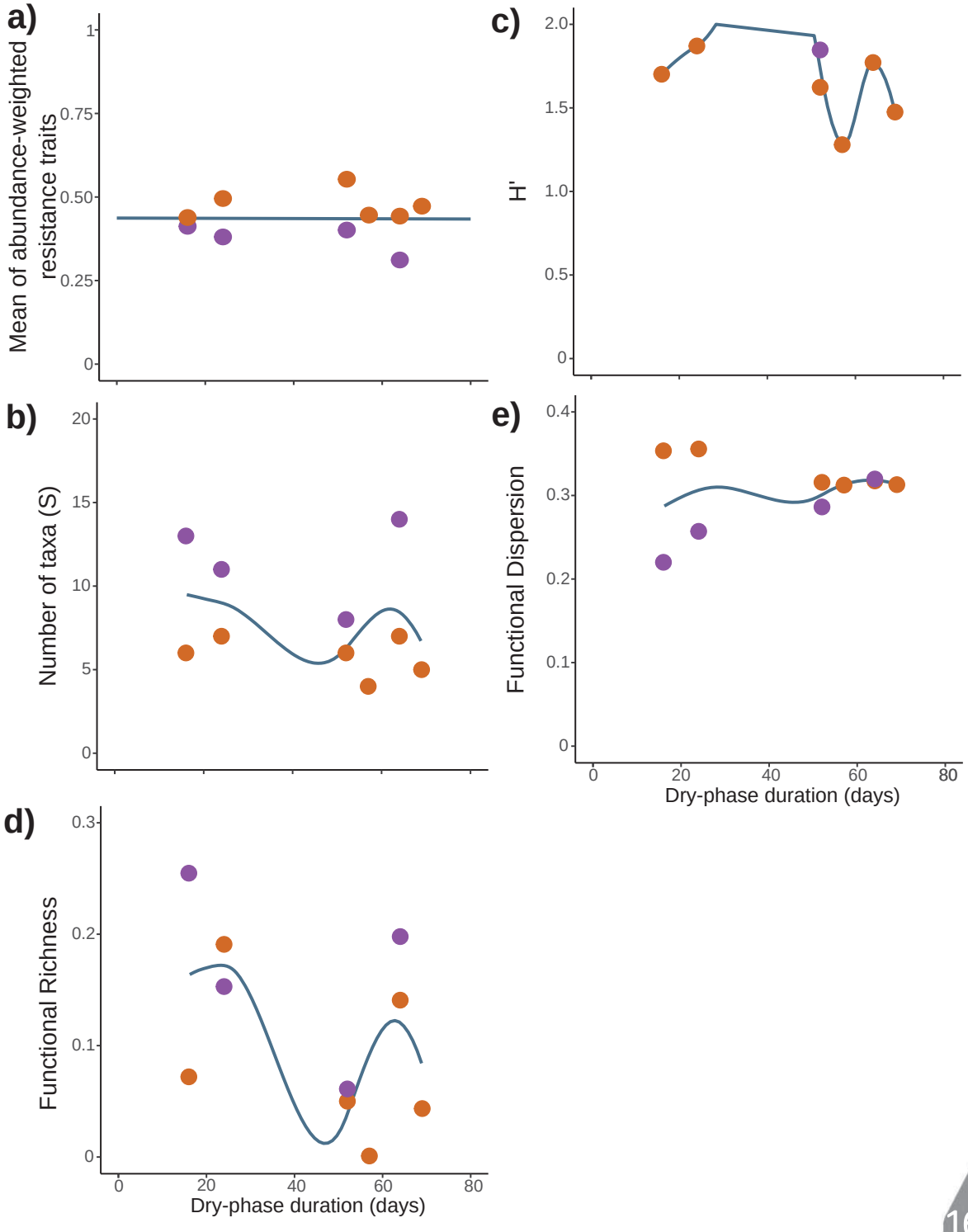


Fig. S2.1. Plots illustrating dry-phase duration against various metrics: a) Mean of abundance-weighted of resistance traits; b) Taxon Richness; c) H', diversity index; d) Functional Richness; e) Functional Dispersion. Lilac points represented hyporheic assemblages, while orange points represented seedbank assemblages. Benthic assembla-ges were excluded. Lines showed possible distribution.



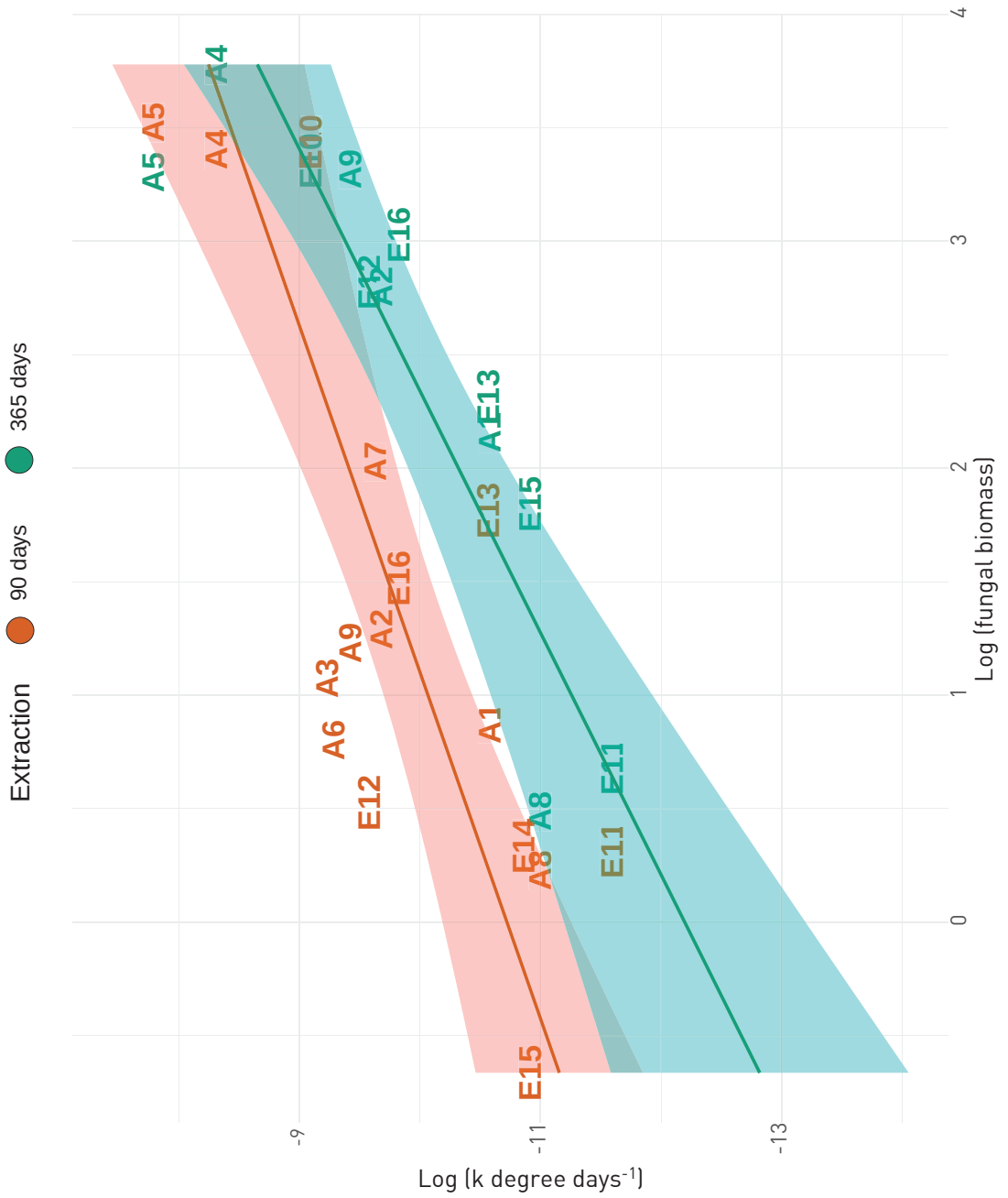


Figure S3.1. Linear relationship between the logarithm of the decomposition rate (degree days -1) and the logarithm of the mean of fungal biomass (mg of fungal biomass/g of AFDM) at each extraction. The marked lines correspond to linear regression, and the dimmest line represents their confidence interval. Orange colour corresponds to the 90-day extraction, while green corresponds to the 1-year extraction

Table S1.1. Selected traits and their respective categories, with selections justified based on their capacity to cope with drying and agricultural conditions (rationale). The 'Database' column indicates the source of each trait.

Trait	Category	↑Drying (rationale)	↑Agriculture (rationale)[j]	Categories_used_functional-metrics	DB
Maximum body size	← 10 mm	Small taxa related to low metabolic demands[a,] and favouring migration to HZ[b]	Favoured	Numerical. Average calculated as the sum of products between the sp proportion at each category and its medium point of each interval category.	1
	→ 10 mm	Associated with long dispersal distances and high fecundity[c]	Unfavoured		1
Life cycle duration	↖ 1 year	Enabling a short life cycle to evade desiccation during dry phase[b]	Favoured	NCREQ1	1
	→1 year		Unfavoured	NCRMO1	
Potential number of reproduction cycles per year	←1		Favoured	SEMIVO	1
	1			UNIVO	
	→1	Enabling to evade desiccation during dry phase[b]	Unfavoured	PLURIVO	
Dispersal	Aquatic passive			AQUPAS	1
	Aquatic active	For active dispersal to recolonize when flow resumes, or to escape drying; and aerial adult stages[d,e]		AQUACT	
	Aerial passive			AERPAS	
	Aerial active	For active dispersal to recolonize when flow resumes, or to escape drying; and aerial adult stages[d,e]		AERACT	
Resistance form	Yes (eggs, stoblasts, gemmules, cocoons, cells, diapause or dormancy)	For inclusion in the invertebrate seedbank[a,d,f]		YES	1
	None			NON	

(continuation)

Trait	Category	↑Drying (rationale)	↑Agriculture (rationale)[j]	Categories_used_functional-metrics	DB
Respiration	Aerial respiration (plastron, spiracle)	Favoured in wet habitats with low oxygen levels due to drying (e.g., isolated pools, HZ)[b,d]		AQUATIC	1
	Aquatic respiration (tegument, gill)			AERIAL	
Locomotion	Flier	For active dispersal to recolonize when flow resumes, or to escape drying; and aerial adult stages[d,e]	Favoured	FLIER	1
	Swimmer	For active dispersal to recolonize when flow resumes, or to escape drying[d]	Unfavoured		
	Crawler	For active dispersal to recolonize when flow resumes, or to escape drying[d]		CRAW	
	Burrower (epibenthic)	Favouring migration to HZ[b]	Favoured	BURR	
	Interstitial (endobenthic)	Favouring migration to HZ[b]	Favoured	INTST	
	Attached		Unfavoured	ATT	
Reproduction	Ovoviviparity	Favouring a reduction in the *in situ* risk of egg mortality[a]	Favoured	OVOV	1
	Isolated eggs or clutches, free		Unfavoured	FREE	
	Isolated eggs or clutches, cemented	Favouring a reduction in the *in situ* risk of egg mortality[g]	Unfavoured	CEM	
	Clutches in vegetation (endophytic)	Favouring a reduction in the *in situ* risk of egg mortality[h]		CLUVEG	
	Clutches, terrestrial	Favouring a reduction in the *in situ* risk of egg mortality[h]	Unfavoured	CLUTER	
	Asexual reproduction		Favoured	ASEX	
Propensity to drift	rare/only during catastrophic events			DRIFT1	2
	occasional			DRIFT2	
	frequent	Passive dispersal to recolonize when flow resumes[i]		DRIFT3	

Table S1.2. Details of each study site, including the season during the sampling campaign (Au, autumn; Wi, winter; Sp, spring; Su, summer); hydrology conditions; water conductivity (µS/cm); water temperature (°C); percentage of water dissolved oxygen (O2%, [O2] concentration); QBR, riparian quality index; IHF, fluvial habitat index; canopy cover (%); and land cover (Urb, urban; Agr, agricultural; and Nat, natural). The dry-phase duration (DD - total days without surface water in the three months prior to the sampling campaign) and dry period (DF) data from the same timeframe were also included. Concentrations of Na, K, Mg, Ca, TOC, Cl, S, F, and DIN (mg/L) were measured.

Code	Reach	Season	Hydrology_conditions	Conductivity	Temperature	O2%	[O2]	pH	QBR	IHF	Canopy	Urb	Agr	Nat	DD
A1.Au	A1	Au	connected	419.3	10.8	101.2	11.23	9.13	95	61	7.03	0.00	3.10	96.90	41
A1.Sp	A1	Sp	connected	369.7	17	102.2	9.6	9.01	95	61	7.03	0.00	3.10	96.90	0
A1.Su	A1	Su	connected	369.8	17.2	88	8.4	8.76	95	61	7.03	0.00	3.10	96.90	0
A1.Wi	A1	Wi	connected	331.2	10.2	96.2	10.81	9.16	95	61	7.03	0.00	3.10	96.90	0
A2.Au	A2	Au	connected	420	10.8	97.2	10.78	8.98	80	75	29.69	0.00	3.10	96.90	27
A2.Sp	A2	Sp	connected	322.5	17.3	78.8	7.5	8.74	80	75	29.69	0.00	3.10	96.90	0
A2.Su	A2	Su	disconnected pools	338.6	21.2	86.8	7.7	8.93	80	69	29.69	0.00	3.10	96.90	0
A2.Wi	A2	Wi	connected	271.8	8.1	92.5	10.88	9.16	80	75	29.69	0.00	3.10	96.90	0
A3.Au	A3	Au	connected	416.8	11.1	101	11.08	9.18	55	72	2.60	0.00	3.10	96.90	53
A3.Sp	A3	Sp	connected	414.5	18.6	88	8.2	8.76	55	72	2.60	0.00	3.10	96.90	0
A3.Su	A3	Su	connected	495	19.6	82.5	7.49	8.42	55	72	2.60	0.00	3.10	96.90	0
A3.Wi	A3	Wi	connected	322.8	9.3	91.5	10.51	9.21	55	72	2.60	0.00	3.10	96.90	0
A4.Au	A4	Au	connected	438.6	10.9	105.1	11.56	9	55	53	0.00	0.00	73.33	26.67	0
A4.Sp	A4	Sp	connected	442.9	16.3	72.3	7.09	8.8	55	53	0.00	0.00	73.33	26.67	0
A4.Su	A4	Su	connected	529	19.5	93	8.13	8.58	55	53	0.00	0.00	73.33	26.67	0
A4.Wi	A4	Wi	connected	363.6	8.9	100.8	11.69	9.03	55	53	0.00	0.00	73.33	26.67	0
A5.Au	A5	Au	connected	460.9	11	106.9	11.78	9.16	10	63	5.73	0.01	57.57	42.41	0
A5.Sp	A5	Sp	connected	492.8	18	92	8.6	8.96	10	63	5.73	0.01	57.57	42.41	0
A5.Su	A5	Su	connected	579	19.1	71.1	6.34	7.62	10	63	5.73	0.01	57.57	42.41	0
A5.Wi	A5	Wi	connected	373.7	7.4	103.6	12.37	9.07	10	63	5.73	0.01	57.57	42.41	0
A6.Au	A6	Au	connected	453.1	10.8	108	11.95	9.06	20	50	0.00	0.01	57.57	42.41	0
A6.Sp	A6	Sp	connected	546	21.5	97.7	8.43	8.93	20	50	0.00	0.01	57.57	42.41	0
A6.Su	A6	Su	disconnected pools	579	19.1	71.1	6.34	7.62	20	40	0.00	0.01	57.57	42.41	37
A6.Wi	A6	Wi	connected	265.2	9.6	110.8	12.59	9.1	20	50	0.00	0.01	57.57	42.41	20
A7.Au	A7	Au	connected	460.6	11.6	107.3	11.66	9.02	10	58	0.00	0.45	47.79	51.76	0
A7.Sp	A7	Sp	connected	524	16.6	62	6	8.68	10	58	0.00	0.45	47.79	51.76	0
A7.Su	A7	Su	dry	NA	NA	NA	NA	NA	10	46	0.00	0.45	47.79	51.76	21
A7.Wi	A7	Wi	connected	383.8	8	95.1	11.24	8.99	10	58	0.00	0.45	47.79	51.76	0
A8.Au	A8	Au	connected	477.7	11.6	101.3	11	9.26	50	52	0.00	0.45	47.79	51.76	79
A8.Sp	A8	Sp	disconnected pools	635	16.7	70	6.5	8.6	50	46	0.00	0.45	47.79	51.76	0

(continuation)

Code	Reach	Season	Hydrology_conditions	Conductivity	Temperature	O2%	[O2]	pH	QBR	IHF	Canopy	Urb	Agr	Nat	DD
A8.Su	A8	Su	disconnected pools	2400	22.7	77.5	6.65	8.11	50	46	0.00	0.45	47.79	51.76	48
A8.Wi	A8	Wi	connected	431.8	8.6	99.3	11.57	9.14	50	52	0.00	0.45	47.79	51.76	0
A9.Au	A9	Au	connected	578.4	12.4	104.6	11.17	9.18	20	69	4.95	0.24	46.73	53.03	80
A9.Sp	A9	Sp	connected	1132	16.8	47	4.5	8.57	20	69	4.95	0.24	46.73	53.03	0
A9.Su	A9	Su	disconnected pools	2050	23.2	96.7	8.25	7.325	20	65	4.95	0.24	46.73	53.03	96
A9.Wi	A9	Wi	connected	587	8.8	78.7	9.12	9.05	20	69	4.95	0.24	46.73	53.03	7
E10.Au	E10	Au	connected	361.7	12.7	96.6	10.2	8.65	95	88	59.38	0.00	33.41	66.59	63
E10.Sp	E10	Sp	connected	297.9	12.6	67.2	7.05	8.37	95	88	59.38	0.00	33.41	66.59	19
E10.Su	E10	Su	connected	320	15.9	77.6	7.62	8.27	95	88	59.38	0.00	33.41	66.59	11
E10.Wi	E10	Wi	connected	292.4	12.1	108.1	11.46	8.43	95	88	59.38	0.00	33.41	66.59	11
E11.Au	E11	Au	dry	NA	NA	NA	NA	NA	95	58	26.56	0.00	0.00	100.00	100
E11.Sp	E11	Sp	dry	NA	NA	NA	NA	NA	95	58	26.56	0.00	0.00	100.00	100
E11.Su	E11	Su	dry	NA	NA	NA	NA	NA	95	58	26.56	0.00	0.00	100.00	100
E11.Wi	E11	Wi	dry	NA	NA	NA	NA	NA	95	58	26.56	0.00	0.00	100.00	100
E12.Au	E12	Au	connected	635	12	69.3	6.9	7.38	80	87	25.78	0.00	0.00	100.00	37
E12.Sp	E12	Sp	connected	521	11.7	64.3	6.96	8.12	80	87	25.78	0.00	0.00	100.00	0
E12.Su	E12	Su	connected	562	17.3	64.4	6.22	7.93	80	87	25.78	0.00	0.00	100.00	0
E12.Wi	E12	Wi	disconnected pools	432.9	10.3	66.4	7.43	7.99	80	75	25.78	0.00	0.00	100.00	0
E13.Au	E13	Au	connected	549	10.6	105.6	10.99	8.24	60	68	13.54	0.00	33.41	66.59	79
E13.Sp	E13	Sp	connected	490.6	11.7	100.1	10.7	9.08	60	68	13.54	0.00	33.41	66.59	0
E13.Su	E13	Su	dry	NA	NA	NA	NA	NA	60	68	13.54	0.00	33.41	66.59	61
E13.Wi	E13	Wi	connected	428.2	8.8	115.2	13.42	9.09	60	68	13.54	0.00	33.41	66.59	0
E14.Au	E14	Au	connected	539	11.7	98.1	9.98	8.17	95	85	35.42	0.00	33.41	66.59	75
E14.Sp	E14	Sp	connected	436.1	17.7	85.4	8.14	8.86	95	85	35.42	0.00	33.41	66.59	16
E14.Su	E14	Su	dry	NA	NA	NA	NA	NA	95	85	35.42	0.00	33.41	66.59	28
E14.Wi	E14	Wi	connected	337.7	7.2	80.9	9.76	8.85	95	85	35.42	0.00	33.41	66.59	9
E15.Au	E15	Au	connected	341	9.4	97.2	11.11	8.78	95	69	26.30	0.00	0.21	99.79	81
E15.Sp	E15	Sp	disconnected pools	521	11.7	64.3	6.96	8.12	95	57	26.30	0.00	0.21	99.79	100
E15.Su	E15	Su	dry	NA	NA	NA	NA	NA	95	51	26.30	0.00	0.21	99.79	100
E15.Wi	E15	Wi	disconnected pools	253.3	7.2	73.2	8.82	8.33	95	57	26.30	0.00	0.21	99.79	81
E16.Au	E16	Au	connected	489	12	103	10.56	8.2	85	61	1.04	0.00	33.41	66.59	7
E16.Sp	E16	Sp	connected	440.3	17	91.3	8.83	8.98	85	61	1.04	0.00	33.41	66.59	0
E16.Su	E16	Su	connected	427.4	20.75	81.6	7.295	8.94	85	61	1.04	0.00	33.41	66.59	0
E16.Wi	E16	Wi	connected	366.3	11.2	106.6	11.7	8.94	85	61	1.04	0.00	33.41	66.59	0

Table S1.3. Relative abundances of taxa by reach and sampling occasion. The taxon codes correspond to those in Table S1.2. Taxon abbreviations are listed in Table S1.4.

Code	AmpEch	AmpGam	AnnHir	AnnOli	BivPis	ColAga	ColBer	ColBid	ColCoe	ColCyp	ColDer	ColDry	ColDys	ColElm	ColEso	ColFElm	ColFHal
A1.Au	0.00	0.00	0.00	0.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A1.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00
A1.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A1.Su	0.00	0.00	0.00	0.97	0.00	0.00	0.00	0.85	0.00	0.00	0.00	2.42	0.00	0.00	0.48	0.00	0.00
A2.Au	0.00	0.13	0.00	12.73	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Wi	0.00	0.00	0.00	0.25	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Sp	0.00	0.00	0.00	1.59	0.00	0.53	0.00	0.00	0.00	0.00	3.17	0.00	0.00	0.00	0.00	0.00	0.00
A2.Su	0.00	0.00	0.00	1.87	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A3.Au	0.00	0.00	0.00	2.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00
A3.Wi	0.00	0.00	0.00	2.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00
A3.Sp	0.00	0.00	0.00	3.62	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.52	0.00	0.00
A3.Su	0.00	0.00	0.00	10.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A4.Au	0.00	0.00	0.00	4.11	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.34	0.00	0.00
A4.Wi	0.00	0.00	0.06	3.05	0.30	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.30	0.00	0.00
A4.Sp	1.07	0.00	0.04	13.17	0.09	0.13	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00
A4.Su	0.27	0.00	0.00	3.23	0.72	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A5.Au	0.00	0.69	0.00	2.37	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00
A5.Wi	0.01	0.00	0.01	7.74	0.00	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.01
A5.Sp	0.58	0.00	0.19	12.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00
A5.Su	12.69	0.00	0.00	4.43	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.95	0.00	0.00
A6.Au	0.00	0.08	0.00	8.66	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00
A6.Wi	0.00	0.00	0.00	7.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A6.Sp	0.00	0.00	0.00	4.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.84	0.00	0.00
A6.Su	0.00	0.00	0.00	38.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Au	0.00	0.00	0.00	1.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.33	0.00	0.00	0.00	0.00
A7.Wi	0.00	0.00	0.00	0.58	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00
A7.Sp	0.00	0.00	0.00	3.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.59	0.73	0.00	0.00
A7.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Au	0.00	0.22	0.00	1.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Wi	0.00	0.00	0.00	5.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00
A8.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

(continuation)

Code	AmpEch	AmpGam	AnnHir	AnnOli	BivPis	ColAga	ColBer	ColBid	ColCoe	ColCyp	ColDer	ColDry	ColDys	ColElm	ColEso	ColFElm	ColFHal
A8.Su	0.00	0.00	0.00	0.96	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Au	0.00	0.00	0.00	2.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Wi	0.00	0.00	0.00	1.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.34	0.00	0.00	0.00	0.00
A9.Sp	0.00	0.00	0.00	4.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.86	0.86	0.00
A9.Su	0.00	0.00	0.00	1.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E10.Au	0.00	0.00	0.00	4.72	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.79	0.00	3.94	3.94	0.00	0.00
E10.Wi	0.00	3.57	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.51	1.53	4.60	0.00	0.00
E10.Sp	0.18	0.61	0.00	5.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.82	7.96	0.00	0.00
E10.Su	0.00	0.47	0.00	1.10	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	3.53	2.28	0.00	0.00
E12.Au	0.00	0.00	0.00	2.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	44.52	0.00	0.00
E12.Wi	0.00	0.00	0.00	0.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.90	0.00	0.00
E12.Sp	0.00	0.00	0.00	1.38	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.04	0.29	0.00	0.00
E12.Su	0.00	0.00	0.00	1.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E13.Au	0.00	1.39	0.00	5.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.69	0.00	0.00
E13.Wi	0.00	0.00	0.00	9.07	0.00	0.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00
E13.Sp	0.00	0.00	0.00	2.51	0.00	0.39	0.00	0.11	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00
E13.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Au	0.00	0.00	0.00	2.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.92	0.00	0.00
E14.Wi	0.00	0.00	0.00	0.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	12.91	0.00	0.00
E14.Sp	0.00	0.00	0.00	0.97	0.00	0.11	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	1.40	0.00	0.00
E14.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Au	0.00	0.00	0.00	5.01	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Wi	0.00	0.00	0.00	1.24	0.00	1.24	0.00	0.00	0.00	0.00	1.24	0.00	0.00	0.00	0.00	0.00	0.00
E15.Sp	0.00	0.00	0.00	17.10	0.00	0.07	0.00	1.07	0.00	0.00	0.00	0.00	0.53	0.00	0.00	0.00	0.00
E15.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E16.Au	0.00	0.33	0.33	14.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.99	0.00	0.00	3.30	0.00	0.00
E16.Wi	0.00	0.00	0.04	4.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.00	0.96	0.00	0.00
E16.Sp	0.00	0.00	0.00	13.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.95	0.00	0.00
E16.Su	0.00	0.00	0.00	1.71	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00

(continuation)

Code	ColFSci	ColGra	ColGyr	ColHal	ColHel	ColHelp	ColHyd	ColHydc	ColHydg	ColHydo	ColHydr	ColHydv	ColHyg	ColIly	ColLac	ColLim	ColMel
A1.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A1.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A1.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.31	0.00	0.00	0.00	2.34	0.00	0.00
A1.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.48	2.67	0.00
A2.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.25	0.00	0.00
A2.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.27	0.00
A3.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00
A3.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A3.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00
A3.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.86	0.00
A4.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A4.Wi	0.00	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.00	0.00	0.00	0.00
A4.Sp	0.00	0.00	0.00	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A4.Su	0.00	0.00	0.00	0.00	0.36	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00
A5.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00
A5.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A5.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A5.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.60	0.00
A6.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A6.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07
A6.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00
A6.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.55	0.18	0.00	0.32	0.00	0.00
A7.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.00	0.00

(continuation)

Code	ColFSci	ColGra	ColGyr	ColHal	ColHel	ColHelp	ColHyd	ColHydc	ColHydg	ColHydo	ColHydr	ColHydv	ColHyg	ColIly	ColLac	ColLim	ColMel
A9.Au	0.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.24	0.00	0.00	0.00
A9.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E10.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.79	0.00	0.00	0.00	0.00	0.00	0.00
E10.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.51	0.00
E10.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.03	0.00
E10.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.26	0.00
E12.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E12.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E12.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.69	0.00	0.00	0.00	0.08	0.04	0.00
E12.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00
E13.Au	0.00	0.00	0.00	0.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E13.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00
E13.Sp	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E13.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.52	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00
E14.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.11
E14.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Wi	0.00	0.00	0.15	0.00	0.00	0.00	1.24	0.00	1.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Sp	0.00	1.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.53	0.00	0.00	0.00	0.00	0.00	0.00
E15.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E16.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.66	0.00	0.00	0.00	0.00	0.33	0.00
E16.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E16.Sp	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.64	0.00
E16.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00

(continuation)

Code	ColNeb	ColOch	ColOre	ColOul	ColPel	ColRio	ColSci	ColSte	ColSti	ColYol	DecAty	DecCam	DecPro	DipAno	DipAth	DipAtr	DipCer
A1.Au	0.00	0.00	0.00	2.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.31	0.00	0.00
A1.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A1.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A1.Su	0.00	0.00	0.00	5.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.97	0.00	0.00
A2.Au	0.00	0.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.27	0.00	0.00
A2.Wi	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00
A3.Au	0.00	0.00	0.00	0.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.26	0.00	0.00	0.00	0.26
A3.Wi	0.00	0.00	0.00	0.81	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00
A3.Sp	0.00	0.00	0.09	0.52	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09
A3.Su	0.00	0.00	0.00	1.29	0.00	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A4.Au	0.00	0.00	0.00	0.93	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A4.Wi	0.00	0.00	0.00	0.36	0.00	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.00	0.00
A4.Sp	0.00	0.00	0.00	2.56	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A4.Su	0.00	0.00	0.00	6.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.18	1.08	0.00	0.00
A5.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00
A5.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00
A5.Sp	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.11	0.00	0.10	0.00	0.19
A5.Su	0.00	0.00	0.00	0.38	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00
A6.Au	0.00	0.00	0.00	2.83	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A6.Wi	0.07	0.00	0.00	9.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A6.Sp	0.00	0.00	0.00	10.22	0.00	0.34	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A6.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Au	0.00	0.00	0.00	41.16	0.00	0.00	0.00	0.38	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.00	0.00
A7.Wi	0.44	0.00	0.00	33.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Sp	0.00	0.00	0.00	59.96	0.00	0.00	0.00	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
A7.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Au	0.00	0.66	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Wi	0.00	0.26	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.23	0.00	0.00	0.00	0.00	0.00	0.00
A8.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	1.76	0.00	0.00	0.00	0.00	0.00	0.00

(continuation)

Code	ColNeb	ColOch	ColOre	ColOul	ColPel	ColRio	ColSci	ColSte	ColSti	ColYol	DecAty	DecCam	DecPro	DipAno	DipAth	DipAtr	DipCer
A9.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.24	0.24	0.00	0.00	0.00	0.00
A9.Wi	0.00	0.00	0.00	5.48	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Sp	0.29	0.00	0.00	2.01	0.00	0.00	0.00	0.57	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33
E10.Au	0.00	0.00	0.00	14.96	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.15	0.00	0.00
E10.Wi	0.00	0.00	0.00	5.11	0.00	0.00	0.00	0.00	0.51	0.00	0.00	0.00	0.00	0.00	3.32	0.00	0.00
E10.Sp	0.00	0.00	0.00	6.41	0.00	0.00	0.00	0.00	0.70	0.00	0.00	0.00	0.00	0.00	0.58	0.00	0.00
E10.Su	0.00	0.00	0.00	15.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.55	0.00	0.00
E12.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.05	0.00	0.00
E12.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.60	0.00	0.00	0.00	0.00	0.00	0.60	0.00	0.00
E12.Sp	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00
E12.Su	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17
E13.Au	0.00	0.00	0.00	1.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.69	0.00	0.00
E13.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00
E13.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E13.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Wi	0.00	0.00	0.00	0.58	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.55	0.00	0.00
E14.Sp	0.00	0.00	0.00	0.54	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Wi	0.00	0.00	0.00	0.15	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Sp	0.00	0.00	0.00	0.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E16.Au	0.00	0.00	0.00	7.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00
E16.Wi	0.00	0.00	0.00	13.77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00
E16.Sp	0.00	0.00	0.00	12.96	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.64	0.00	0.00
E16.Su	0.00	0.00	0.00	1.54	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.34	2.05	0.00

(continuation)

Code	DipCera	DipChirn	DipClin	DipCuli	DipDasy	DipDix	DipDixa	DipDol	DipEri	DipFAth	DipFDix	DipFLim	DipFor	DipFSim	DipHem	DipHex
A1.Au	21.44	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A1.Wi	8.74	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.36	0.00
A1.Sp	9.05	0.00	0.00	0.00	0.00	0.00	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.94	0.00	0.00
A1.Su	21.94	0.85	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.00
A2.Au	16.98	1.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Wi	14.36	0.25	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00
A2.Sp	13.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Su	77.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A3.Au	5.54	0.77	0.00	0.00	0.13	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.19	3.09	0.00	0.00
A3.Wi	1.34	0.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	15.32	0.00	0.00
A3.Sp	0.86	2.24	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00
A3.Su	7.89	7.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A4.Au	6.45	0.44	0.00	0.00	0.00	0.00	0.00	0.05	0.15	0.00	0.00	0.00	0.00	0.29	0.00	0.00
A4.Wi	5.21	4.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.52	0.00	0.00
A4.Sp	0.34	0.77	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.34	0.00	0.00
A4.Su	4.98	3.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.08	0.54	0.00
A5.Au	1.97	0.10	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.39	0.00
A5.Wi	1.34	0.73	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.57	0.00	17.24	0.01	0.00
A5.Sp	0.00	1.31	0.19	0.00	0.00	0.00	3.31	0.00	0.00	0.00	0.10	0.00	0.00	1.56	0.00	0.00
A5.Su	0.38	7.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.96	0.38	0.00
A6.Au	1.17	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.08	0.00	0.17	0.00	0.00
A6.Wi	0.50	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00
A6.Sp	0.17	2.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	16.58	0.00	0.17
A6.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00
A7.Wi	0.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.44	0.00	0.00
A7.Sp	0.41	0.32	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00
A7.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Au	3.07	1.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	0.00	0.00
A8.Wi	3.42	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.98	0.00	0.00
A8.Sp	1.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Su	7.88	0.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Au	0.71	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Wi	0.68	1.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.74	0.00	0.00

(continuation)

Code	DipCera	DipChirn	DipClin	DipCuli	DipDasy	DipDix	DipDixa	DipDol	DipEri	DipFAth	DipFDix	DipFLim	DipFor	DipFSim	DipHem	DipHex
A9.Sp	0.00	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Su	0.00	2.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E10.Au	0.79	0.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E10.Wi	0.17	0.34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.34	0.00	0.00
E10.Sp	0.18	0.64	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00
E10.Su	3.38	0.31	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.39	0.00
E12.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E12.Wi	0.15	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E12.Sp	2.16	0.00	0.00	0.00	0.00	0.73	0.00	0.00	0.00	0.00	0.00	0.65	0.00	2.97	0.00	0.04
E12.Su	33.88	0.33	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E13.Au	3.47	1.39	0.00	0.00	0.00	0.00	0.69	0.00	0.00	0.00	0.00	0.00	0.00	2.08	1.39	0.00
E13.Wi	2.59	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00
E13.Sp	2.15	0.25	0.25	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	2.91	0.00	0.00
E13.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Au	6.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Wi	33.89	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.39	0.00
E14.Sp	6.56	0.11	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	4.73	0.00	0.11
E14.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Au	1.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00
E15.Wi	1.24	2.47	0.00	0.00	0.00	1.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Sp	0.53	0.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E16.Au	2.64	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.66	0.00	0.00	0.00	0.33	0.66	0.00
E16.Wi	4.55	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	3.15	0.04	0.00
E16.Sp	0.81	0.81	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.21	0.08	0.00
E16.Su	12.12	0.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

(continuation)

Code	DipCera	DipChirn	DipClin	DipCuli	DipDasy	DipDix	DipDixa	DipDol	DipEri	DipFAth	DipFDix	DipFLim	DipFor	DipFSim	DipHem	DipHex
A1.Au	21.44	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A1.Wi	8.74	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.36	0.00
A1.Sp	9.05	0.00	0.00	0.00	0.00	0.00	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.94	0.00	0.00
A1.Su	21.94	0.85	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.00
A2.Au	16.98	1.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Wi	14.36	0.25	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00
A2.Sp	13.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Su	77.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A3.Au	5.54	0.77	0.00	0.00	0.13	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.19	3.09	0.00	0.00
A3.Wi	1.34	0.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	15.32	0.00	0.00
A3.Sp	0.86	2.24	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00
A3.Su	7.89	7.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A4.Au	6.45	0.44	0.00	0.00	0.00	0.00	0.00	0.05	0.15	0.00	0.00	0.00	0.00	0.29	0.00	0.00
A4.Wi	5.21	4.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.52	0.00	0.00
A4.Sp	0.34	0.77	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.34	0.00	0.00
A4.Su	4.98	3.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.08	0.54	0.00
A5.Au	1.97	0.10	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.39	0.00
A5.Wi	1.34	0.73	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.57	0.00	17.24	0.01	0.00
A5.Sp	0.00	1.31	0.19	0.00	0.00	0.00	3.31	0.00	0.00	0.00	0.10	0.00	0.00	1.56	0.00	0.00
A5.Su	0.38	7.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.96	0.38	0.00
A6.Au	1.17	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.08	0.00	0.17	0.00	0.00
A6.Wi	0.50	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00
A6.Sp	0.17	2.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	16.58	0.00	0.17
A6.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00
A7.Wi	0.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.44	0.00	0.00
A7.Sp	0.41	0.32	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00
A7.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Au	3.07	1.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	0.00	0.00
A8.Wi	3.42	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.98	0.00	0.00
A8.Sp	1.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Su	7.88	0.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

(continuation)

Code	DipCera	DipChirn	DipClin	DipCuli	DipDasy	DipDix	DipDixa	DipDol	DipEri	DipFAth	DipFDix	DipFLim	DipFor	DipFSim	DipHem	DipHex
A9.Au	0.71	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Wi	0.68	1.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.74	0.00	0.00
A9.Sp	0.00	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Su	0.00	2.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E10.Au	0.79	0.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E10.Wi	0.17	0.34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.34	0.00	0.00
E10.Sp	0.18	0.64	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00
E10.Su	3.38	0.31	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.39	0.00
E12.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E12.Wi	0.15	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E12.Sp	2.16	0.00	0.00	0.00	0.00	0.73	0.00	0.00	0.00	0.00	0.00	0.65	0.00	2.97	0.00	0.04
E12.Su	33.88	0.33	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E13.Au	3.47	1.39	0.00	0.00	0.00	0.00	0.69	0.00	0.00	0.00	0.00	0.00	0.00	2.08	1.39	0.00
E13.Wi	2.59	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00
E13.Sp	2.15	0.25	0.25	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	2.91	0.00	0.00
E13.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Au	6.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Wi	33.89	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.39	0.00
E14.Sp	6.56	0.11	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	4.73	0.00	0.11
E14.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Au	1.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00
E15.Wi	1.24	2.47	0.00	0.00	0.00	1.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Sp	0.53	0.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E16.Au	2.64	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.66	0.00	0.00	0.00	0.33	0.66	0.00
E16.Wi	4.55	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	3.15	0.04	0.00
E16.Sp	0.81	0.81	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.21	0.08	0.00
E16.Su	12.12	0.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

(continuation)

Code	DipLim	DipOrth	DipPed	DipPro	DipProd	DipPsy	DipPty	DipRha	DipSci	DipSim	DipStr	DipSyr	DipTab	DipTant	DipTany	DipTip	EphAce
A1.Au	0.00	3.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.31	0.00	0.25	0.25	1.74	0.06	0.00
A1.Wi	0.18	61.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.46	0.00	0.00	0.73	1.91	0.00	0.00
A1.Sp	0.00	46.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.31	0.00	0.00	0.16	0.94	0.00	0.00
A1.Su	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.36	0.00	0.12	1.33	6.42	0.00	0.00
A2.Au	0.00	2.92	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.80	8.89	0.13	0.00
A2.Wi	0.00	7.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.01	0.00	0.25	1.76	2.77	0.00	0.00
A2.Sp	0.00	9.52	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.53	0.00	0.00	1.59	2.65	3.17	0.00
A2.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.87	5.86	0.00	0.00
A3.Au	0.00	52.41	0.00	0.26	0.00	0.06	0.13	0.13	0.06	0.00	0.00	0.00	0.13	2.12	4.19	0.13	0.00
A3.Wi	0.00	36.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.16	1.51	2.00	0.00	0.20
A3.Sp	0.09	32.04	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.39	14.30	0.00	0.00
A3.Su	0.31	0.82	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.80	26.64	0.00	0.00
A4.Au	0.00	61.32	0.00	0.00	0.00	0.29	0.00	0.00	0.00	0.00	0.15	0.00	0.20	1.96	1.71	0.39	0.00
A4.Wi	0.00	36.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.61	1.86	0.00	0.00
A4.Sp	0.00	7.37	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.33	3.28	0.38	0.00
A4.Su	0.00	2.60	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.54	0.00	0.00	8.56	23.05	0.00	0.00
A5.Au	0.00	83.51	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	2.67	0.20	0.49	0.00
A5.Wi	0.00	57.82	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	4.11	1.74	0.00	0.00
A5.Sp	0.05	7.93	0.88	0.44	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	10.94	2.24	0.10	0.00
A5.Su	0.00	5.86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.00	0.00	15.77	3.45	0.00	0.00
A6.Au	0.00	74.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.17	6.16	0.00	0.00	0.00
A6.Wi	0.00	24.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.14	8.37	0.86	0.00	0.00
A6.Sp	0.17	26.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	9.05	3.69	0.00	0.00
A6.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.56	0.00	0.00
A7.Au	0.00	46.87	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.22	0.00	0.00
A7.Wi	0.00	15.57	0.00	0.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.05	0.11
A7.Sp	0.00	7.30	0.55	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.43	0.91	0.14	0.00
A7.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Au	0.00	84.87	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.66	0.22	0.00	0.00
A8.Wi	0.00	32.37	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	28.01	1.96	0.00	0.00
A8.Sp	0.00	5.63	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.04	15.49	0.00	0.00
A8.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	43.95	2.87	0.00	0.00

(continuation)

Code	DipLim	DipOrth	DipPed	DipPro	DipProd	DipPsy	DipPty	DipRha	DipSci	DipSim	DipStr	DipSyr	DipTab	DipTant	DipTany	DipTip	EphAce
A9.Au	0.00	67.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.80	1.43	0.00	0.00
A9.Wi	0.00	35.27	0.00	0.00	0.00	0.00	0.00	0.34	0.00	0.00	0.34	0.00	0.00	5.14	6.16	0.00	0.00
A9.Sp	0.00	6.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.15	3.74	0.00	0.00
A9.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	13.14	0.99	0.11	0.00
E10.Au	0.00	11.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.94	0.00	0.00	2.36	4.72	0.00	0.00
E10.Wi	0.00	6.13	0.00	0.00	0.00	0.00	0.00	0.34	0.00	0.00	0.00	0.00	0.00	1.36	6.21	0.17	0.00
E10.Sp	0.00	17.07	0.00	0.00	0.12	1.21	0.00	0.00	0.00	0.00	0.52	0.00	0.00	1.28	0.82	0.03	0.00
E10.Su	0.00	10.36	0.00	0.00	0.00	1.18	0.00	0.00	0.00	0.00	0.47	0.00	0.00	19.47	3.38	0.08	0.00
E12.Au	1.37	10.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.74	0.00	0.00
E12.Wi	0.00	45.37	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.19	7.01	0.00	0.00
E12.Sp	0.00	43.38	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	12.34	7.09	0.12	0.00
E12.Su	0.00	5.62	0.00	0.00	0.66	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	19.01	14.71	0.00	0.00
E13.Au	1.39	45.14	0.00	0.00	0.00	1.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.56	5.56	1.39	0.00
E13.Wi	0.00	50.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.69	0.35	0.00	0.78	2.50	0.00	0.00
E13.Sp	0.04	67.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	5.95	3.73	0.00	0.00
E13.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Au	0.00	7.83	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.00	0.23	0.23	2.30	0.00	0.00
E14.Wi	0.26	6.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.32	0.00	0.00	0.13	10.91	0.00	0.00
E14.Sp	0.00	15.38	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	1.08	0.00	0.00	1.29	2.80	0.11	0.00
E14.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Au	0.00	48.58	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.14	0.00
E15.Wi	0.00	1.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.24	0.00	0.00
E15.Sp	0.00	0.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.53	0.00	2.67	0.00	0.00
E15.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E16.Au	0.00	27.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.66	0.00	0.66	0.66	0.66	0.00	0.00
E16.Wi	0.09	23.48	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.04	2.14	1.31	0.00	0.00
E16.Sp	0.16	2.74	0.00	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.40	2.42	0.32	0.00
E16.Su	0.00	0.34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.34	41.30	0.00	0.00

(continuation)

Code	EphBae	EphCae	EphCen	EphCho	EphClo	EphEcd	EphEphl	EphFBae	EphFHep	EphHab	EphHabp	EphHep	EphLep	EphPar	EphPro	EphThr
A1.Au	2.98	57.80	0.25	0.00	0.00	0.00	0.00	0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A1.Wi	2.09	0.00	0.00	0.00	0.00	0.09	0.00	0.36	0.00	0.55	0.00	0.00	0.36	0.18	0.00	0.00
A1.Sp	30.27	0.31	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.16	0.00	0.00	0.00	0.00	0.00	0.00
A1.Su	0.00	16.24	0.00	0.00	0.85	0.00	0.00	6.67	0.00	0.48	0.00	0.00	0.00	0.00	0.00	0.12
A2.Au	0.93	39.12	0.00	0.00	0.00	0.00	0.00	4.51	0.13	0.00	0.00	0.00	0.13	0.00	0.00	2.52
A2.Wi	0.00	55.16	0.00	0.00	0.50	0.50	0.00	0.76	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Sp	7.41	11.64	0.00	0.00	0.00	0.00	0.00	0.00	0.00	15.34	0.00	0.00	0.00	0.00	0.00	0.00
A2.Su	0.00	2.66	0.00	0.00	0.00	0.00	0.00	2.13	0.00	0.27	0.00	0.00	0.00	0.00	0.00	6.40
A3.Au	3.41	7.53	0.00	0.00	0.19	0.06	0.06	0.52	0.06	0.77	1.61	0.00	0.71	0.00	4.25	0.00
A3.Wi	11.36	2.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	18.29	0.00	0.00	0.00	0.00	0.00	0.04
A3.Sp	4.48	3.53	0.00	0.00	0.00	0.00	0.00	1.72	0.00	25.06	0.00	0.00	0.00	0.00	0.00	0.00
A3.Su	0.00	24.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.43	4.00
A4.Au	4.79	2.59	0.00	0.00	0.39	0.00	0.00	0.00	0.00	3.37	0.00	0.00	0.10	0.00	3.47	0.05
A4.Wi	21.44	1.44	0.00	0.00	0.12	0.00	0.42	0.00	0.00	0.00	0.00	0.00	0.84	0.00	1.92	0.00
A4.Sp	12.95	0.43	0.00	0.00	0.68	0.00	4.05	0.17	0.00	1.79	0.00	0.00	0.00	0.00	0.00	0.00
A4.Su	1.79	10.03	0.00	0.00	0.00	0.00	0.00	1.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A5.Au	0.99	2.67	0.00	0.00	0.89	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A5.Wi	0.40	1.07	0.00	0.00	0.00	0.00	0.00	0.39	0.00	1.54	0.00	0.00	0.77	0.00	0.00	0.00
A5.Sp	22.32	0.73	0.00	0.00	0.68	0.05	0.97	0.00	0.00	11.96	0.00	0.00	0.00	0.00	0.00	0.05
A5.Su	6.53	5.33	0.00	0.15	0.00	0.00	0.00	0.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08
A6.Au	0.17	1.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A6.Wi	0.29	1.50	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.72	0.00	0.00	0.21	0.00	0.36	0.00
A6.Sp	4.69	0.00	0.00	0.00	0.00	2.85	0.17	0.84	0.00	0.34	0.00	0.00	0.00	0.00	0.00	0.00
A6.Su	0.00	53.75	0.00	0.00	0.00	0.00	0.00	1.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Au	0.05	0.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Wi	0.95	0.22	0.00	0.00	0.00	0.00	0.00	1.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Sp	3.65	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.68	0.00	0.00	0.00	0.00	0.05	0.00
A7.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Au	0.88	0.44	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Wi	3.42	0.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Sp	0.00	33.80	0.00	0.00	32.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Su	0.00	23.89	0.00	0.39	0.00	0.00	0.72	3.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

(continuation)

Code	EphBae	EphCae	EphCen	EphCho	EphClo	EphEcd	EphEphl	EphFBae	EphFHep	EphHab	EphHabp	EphHep	EphLep	EphPar	EphPro	EphThr
A9.Au	0.00	1.43	0.00	0.00	0.00	0.00	0.00	0.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Wi	3.08	0.00	0.00	0.00	0.00	0.68	0.00	0.00	0.00	0.68	0.00	0.00	0.00	0.00	0.00	0.00
A9.Sp	1.44	1.72	0.00	0.00	68.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Su	0.00	81.60	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E10.Au	0.00	5.51	0.00	0.00	0.00	2.36	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.87	0.00	0.00
E10.Wi	0.26	3.74	0.00	0.00	0.00	0.43	3.91	0.00	0.00	8.51	0.00	0.17	0.00	8.17	0.00	0.00
E10.Sp	0.88	0.30	0.00	0.00	0.00	0.06	12.63	0.18	0.00	9.69	0.00	0.00	0.00	1.58	0.00	0.12
E10.Su	0.16	0.16	0.78	0.00	0.00	0.00	0.63	2.28	0.00	0.47	0.00	0.00	0.00	0.24	0.00	0.00
E12.Au	0.00	0.00	0.00	0.00	0.00	2.74	0.00	0.00	0.00	0.00	0.00	0.00	17.12	8.22	0.00	0.00
E12.Wi	0.00	0.00	1.34	0.00	0.60	0.30	0.00	0.00	0.00	4.48	0.00	0.00	0.00	5.22	0.00	0.00
E12.Sp	0.29	0.08	0.00	0.00	0.16	0.08	0.08	0.00	0.00	4.77	0.00	0.00	0.00	0.49	0.00	0.00
E12.Su	0.00	0.00	0.66	0.00	0.66	0.00	0.00	3.64	0.00	3.97	0.00	0.00	0.00	0.00	0.00	0.00
E13.Au	2.08	0.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.69	0.00	0.00
E13.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.52	0.00	6.39	0.00	0.00	0.00	0.00	0.00	0.00
E13.Sp	1.97	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	3.55	0.00	0.00	0.00	0.00	0.00	0.00
E13.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Au	0.00	12.90	6.22	0.00	0.00	1.38	0.00	0.00	0.00	2.30	0.00	0.00	0.00	0.00	0.00	0.23
E14.Wi	7.68	3.16	0.13	0.00	0.00	2.39	0.13	2.84	0.00	7.94	0.00	0.00	0.00	0.00	0.00	0.00
E14.Sp	11.83	2.80	0.00	0.00	0.00	0.54	0.65	0.75	0.00	17.74	0.00	0.00	0.00	0.43	0.00	0.32
E14.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Au	0.00	0.95	0.00	0.00	0.81	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.57	0.00
E15.Wi	0.00	17.31	0.00	0.00	13.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	30.91
E15.Sp	0.00	5.34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.14	0.00	0.00	0.00	0.00	0.00	44.89
E15.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E16.Au	0.33	3.30	0.66	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.66
E16.Wi	12.24	4.24	0.00	0.00	0.00	0.00	3.24	0.00	0.00	8.40	0.00	0.00	3.89	0.00	0.00	0.04
E16.Sp	15.30	0.81	0.00	0.00	0.00	0.08	2.98	0.97	0.00	24.24	0.00	0.00	0.00	0.00	0.00	0.00
E16.Su	0.00	5.80	0.00	0.00	0.17	0.00	0.00	17.58	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.85

(continuation)

Code	GasAnc	GasBit	GasByt	GasByts	GasFAnc	GasFByt	GasFPhy	GasGal	GasHyd	GasLym	GasPhy	GasPhyl	GasPot	GasRad	GasVal	HemAqu
A1.Au	0.31	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A1.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A1.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A1.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Au	0.27	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A3.Au	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A3.Wi	0.04	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A3.Sp	0.09	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A3.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A4.Au	0.15	0.00	0.00	0.00	0.00	0.83	0.05	0.00	0.05	0.05	0.05	0.00	0.00	0.00	0.00	0.00
A4.Wi	0.00	0.00	0.00	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.03	0.00	0.30	0.00	0.06	0.00
A4.Sp	8.35	0.00	0.00	0.00	0.00	0.00	0.00	7.63	0.00	0.00	5.11	0.00	0.00	1.53	0.00	0.00
A4.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	12.64	0.00	0.00	2.33	0.00	0.00	0.00	0.00	0.00
A5.Au	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00
A5.Wi	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.00	0.00	0.00	0.00
A5.Sp	6.96	0.00	0.00	0.00	0.00	0.29	0.00	0.00	0.19	0.00	1.26	0.00	0.00	0.00	0.00	0.00
A5.Su	6.08	0.00	0.00	0.00	0.00	0.00	0.00	7.73	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00
A6.Au	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A6.Wi	0.43	0.07	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A6.Sp	8.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00
A6.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Au	2.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	2.20	0.00	0.00	0.00	0.00
A7.Wi	3.69	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	1.64	0.00	0.22	0.00	0.00
A7.Sp	8.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.23	0.00	0.00	0.00	0.00	0.00
A7.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

(continuation)

Code	GasAnc	GasBit	GasByt	GasByts	GasFAnc	GasFByt	GasFPhy	GasGal	GasHyd	GasLym	GasPhy	GasPhyl	GasPot	GasRad	GasVal	HemAqu
A9.Au	1.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.61	0.00	0.24	0.00	0.00
A9.Wi	9.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.34	3.42	0.00	0.00	0.00	0.00
A9.Sp	0.86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E10.Au	8.66	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.36	0.00	0.00
E10.Wi	1.45	0.00	0.00	0.00	6.21	0.34	0.00	0.00	0.85	0.68	0.00	0.00	0.00	0.17	0.00	0.09
E10.Sp	2.88	0.00	0.36	0.00	0.00	0.94	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E10.Su	7.06	0.00	0.00	0.00	0.00	0.55	0.00	2.12	0.00	0.00	0.00	0.00	0.00	0.24	0.00	0.00
E12.Au	2.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.68	0.00	0.00
E12.Wi	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E12.Sp	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.57	0.65	0.00	0.00
E12.Su	1.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00
E13.Au	3.47	0.69	0.00	0.00	0.00	0.00	0.00	0.00	4.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E13.Wi	0.00	0.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E13.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E13.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Au	0.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.00	0.00	0.00	0.00
E14.Wi	0.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.06	0.00	0.06
E14.Sp	0.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.11	0.00	0.00
E14.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.24	0.00	0.00	0.00	0.00	0.00
E15.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E16.Au	0.99	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E16.Wi	0.52	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00
E16.Sp	2.66	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E16.Su	0.00	0.00	0.00	1.54	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

(continuation)

Code	HemArc	HemCor	HemGer	HemHyd	HemMic	HemMict	HemNau	HemNot	HemPle	HemVel	MegSia	Nem	OdoAes	OdoAna	OdoBoy	OdoCal
A1.Au	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00
A1.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.00
A1.Sp	0.00	0.00	0.00	0.16	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A1.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.93	0.00	0.00	0.00	0.00
A2.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00
A2.Sp	0.00	0.00	0.00	0.00	0.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A3.Au	0.00	0.00	0.00	0.00	0.00	0.64	0.00	0.00	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.00
A3.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00
A3.Sp	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.09	0.00	0.00	0.17	0.17	0.00	0.00	0.34	0.09
A3.Su	0.00	0.00	0.00	0.00	0.31	0.31	0.00	0.00	0.00	0.00	0.24	0.00	0.00	0.00	0.12	0.00
A4.Au	0.00	0.00	0.00	0.00	0.00	0.29	0.15	0.00	0.05	0.00	0.00	1.76	0.00	0.00	0.00	0.00
A4.Wi	0.00	0.00	0.00	0.00	0.00	10.66	0.00	0.00	0.00	0.00	0.03	0.24	0.00	0.00	0.00	0.12
A4.Sp	0.00	0.00	0.17	0.00	0.17	0.00	0.00	0.13	0.00	0.00	0.00	0.34	0.00	0.00	0.00	0.00
A4.Su	0.00	0.00	0.00	0.00	0.18	2.66	0.00	0.00	0.00	0.00	0.00	1.26	0.00	0.00	0.00	0.00
A5.Au	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.79	0.00	0.00	0.00	0.00
A5.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.00	0.00	0.00	0.00
A5.Sp	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00
A5.Su	0.00	0.00	0.08	0.00	0.15	0.15	0.00	0.00	0.00	0.00	0.00	0.38	0.00	0.00	0.00	0.00
A6.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.50	0.00	0.00	0.00	0.00
A6.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.43	0.00	0.00	0.00	0.00
A6.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00
A6.Su	0.00	0.00	0.00	0.00	0.00	1.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00
A7.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Sp	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.00	0.00	0.00	0.00
A7.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.34	0.00	0.00	0.00	0.00
A8.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Su	0.00	0.00	0.00	0.00	0.00	10.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.24	0.00	0.00

(continuation)

Code	HemArc	HemCor	HemGer	HemHyd	HemMic	HemMict	HemNau	HemNot	HemPle	HemVel	MegSia	Nem	OdoAes	OdoAna	OdoBoy	OdoCal
A9.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E10.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E10.Wi	0.00	0.00	0.17	0.00	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00
E10.Sp	0.12	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00
E10.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	6.36	0.00	0.00	0.08	0.00
E12.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.37	0.00
E12.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E12.Sp	0.00	0.00	0.00	0.04	0.33	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.12	0.00	0.00	0.00
E12.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E13.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.39	0.00	3.47	0.00	0.00	0.00	0.00
E13.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	1.21	0.00	0.00	0.00	0.00
E13.Sp	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.32	0.00	0.00	0.00	0.00
E13.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	46.54	0.00	0.00	0.00	0.00
E14.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Sp	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.97	0.00
E14.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.54	0.00	0.00	0.00	0.00
E15.Wi	0.00	2.47	0.00	0.00	0.15	0.00	0.15	1.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Sp	0.00	0.00	0.00	0.00	0.00	0.00	3.21	1.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E16.Au	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.33	0.00
E16.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00
E16.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00
E16.Su	0.00	0.00	0.17	0.00	0.00	4.78	0.00	0.00	0.00	0.00	0.17	0.00	0.17	0.00	0.00	0.00

(continuation)

Code	OdoCoe	OdoCor	OdoFCoe	OdoFCor	OdoFGom	OdoFLes	OdoGom	OdoLes	OdoLib	OdoMac	OdoOny	OdoOrt	OdoOxy	OdoPla	OdosAno	OdoSl
A1.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.62	0.00	0.00	0.25	0.00	0.00
A1.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A1.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A1.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.00	0.00	0.00	1.33	0.00	0.00	0.00	0.00	0.48
A2.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.27	0.00	3.85	0.00	0.00	0.00
A2.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	1.76	0.00	0.00	0.00
A2.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.53	4.76	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.53	0.00	0.00	0.00	0.00	0.00
A3.Au	0.00	0.26	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.06	0.19	0.00	0.00
A3.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.04	0.00	0.04	0.00	0.00	0.00
A3.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00
A3.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.26	0.00	0.00	0.00	0.00	0.55
A4.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.10	0.00	0.20	0.20	0.00	0.00
A4.Wi	0.00	0.00	0.00	0.06	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.12	0.00
A4.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A4.Su	0.00	0.38	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.61	0.00	0.00	0.00	0.00	0.18
A5.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00
A5.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A5.Sp	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A5.Su	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.08
A6.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A6.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A6.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A6.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.63	0.00	0.00	0.00	2.50	0.00	0.00	0.00	0.00	0.31
A7.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Wi	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.00
A8.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00
A8.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.12	0.00	0.00	0.24	0.00	0.00	0.00	0.00	0.24

(continuation)

Code	OdoCoe	OdoCor	OdoFCoe	OdoFCor	OdoFGom	OdoFLes	OdoGom	OdoLes	OdoLib	OdoMac	OdoOny	OdoOrt	OdoOxy	OdoPla	OdosAno	OdoSl
A9.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E10.Au	0.00	1.57	0.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E10.Wi	0.00	1.02	0.00	0.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E10.Sp	0.00	0.12	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.00	0.00
E10.Su	0.00	2.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.90	0.00	0.00	0.00	0.00	0.00
E12.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E12.Wi	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	2.69
E12.Sp	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.04	0.04	0.00	0.00	0.00	0.04	0.04	0.00	0.00
E12.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33
E13.Au	0.00	0.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.69	0.00	0.00	0.00	0.00	0.00
E13.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E13.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.39	0.07	0.00	0.00
E13.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.00	0.92	0.00	0.00	0.00
E14.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.00	0.06	0.00	0.00	0.26
E14.Sp	0.00	0.00	0.00	0.00	0.00	2.15	0.11	0.11	0.00	0.00	0.00	0.00	1.40	0.00	0.00	0.11
E14.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Au	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.24	0.00	0.00	0.00	0.00
E15.Sp	0.00	0.00	0.00	0.00	0.00	10.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E16.Au	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E16.Wi	0.00	0.00	0.00	0.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00
E16.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E16.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.85	0.00	0.00	0.34	0.00	0.00

(continuation)

Code	OdoSym	OdoSymf	OdosZyg	PleCap	PleCapn	PleFCap	PleFPer	PleHem	PleIso	PleLeu	PleNem	PlePer	PleSI	Tri	TriAgr	TriCal	TriChe
A1.Au	0.00	0.00	0.00	0.31	0.00	0.00	0.00	0.00	0.00	1.99	0.00	0.00	0.00	0.06	0.00	0.00	0.00
A1.Wi	0.00	0.00	0.00	1.82	0.00	0.00	0.00	0.00	0.00	9.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A1.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.90	0.16	0.00	0.00	0.00	0.00	0.00	0.00
A1.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	24.36	0.61	0.00	0.00	0.12	0.00	0.00	0.00
A2.Au	0.00	0.00	0.00	0.00	2.25	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Wi	0.00	0.00	0.00	1.01	4.79	0.00	0.00	0.00	0.00	0.00	3.53	0.00	0.50	0.25	0.00	0.00	0.00
A2.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	21.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A3.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.16	3.86	0.00	0.00	0.19	0.00	0.00	0.00
A3.Wi	0.00	0.00	0.00	0.98	0.00	0.00	0.00	0.61	0.00	0.00	1.59	0.00	0.00	0.00	0.00	0.00	0.00
A3.Sp	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	1.64	0.52	0.00	0.00	0.00	0.00	0.00	0.00
A3.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A4.Au	0.00	0.00	0.00	0.20	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.98	0.00	0.00	0.00
A4.Wi	0.00	0.00	0.06	1.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.00	0.03	0.18	0.00	0.03
A4.Sp	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	4.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A4.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.50	0.00	0.00	0.00	1.08	0.00	0.00	0.00
A5.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.20	0.00	0.00	0.00
A5.Wi	0.00	0.00	0.00	0.00	0.34	0.00	0.00	0.06	0.00	0.07	1.03	0.11	0.04	0.00	0.00	0.00	0.00
A5.Sp	0.00	0.00	0.00	0.49	0.00	0.00	0.00	0.00	0.00	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A5.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.28	0.00	0.00	0.00	0.68	0.00	0.00	0.00
A6.Au	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	1.08	0.00	0.00	0.00	0.00	0.00	0.00
A6.Wi	0.00	0.00	0.00	4.86	0.00	0.00	0.00	1.00	0.00	0.00	35.62	1.65	0.00	0.00	0.00	0.00	0.00
A6.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A6.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Au	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	2.58	0.00	0.00	0.00	0.00	0.00	0.00
A7.Wi	0.00	0.00	0.00	0.22	0.00	0.00	0.00	0.99	0.22	0.44	26.75	9.72	0.00	0.15	0.00	0.00	0.00
A7.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.36	0.46	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00
A7.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Au	0.00	0.00	0.00	3.95	0.00	0.00	0.00	0.00	0.00	0.22	0.88	0.00	0.00	0.00	0.00	0.00	0.00
A8.Wi	0.00	0.00	0.00	14.60	0.00	0.00	0.00	0.43	0.00	0.51	0.34	0.34	0.00	0.00	0.00	0.00	0.00
A8.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Su	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

(continuation)

Code	OdoSym	OdoSymf	OdosZyg	PleCap	PleCapn	PleFCap	PleFPer	PleHem	PleIso	PleLeu	PleNem	PlePer	PleSI	Tri	TriAgr	TriCal	TriChe
A9.Au	0.00	0.00	0.00	10.93	0.00	0.00	0.00	0.00	0.00	0.00	4.75	0.00	0.00	0.00	0.00	0.00	0.00
A9.Wi	0.00	0.00	0.00	14.73	0.00	0.00	0.00	5.14	0.00	0.00	0.00	0.68	0.00	0.00	0.00	0.00	0.00
A9.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E10.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.09	0.00	0.00	0.00	3.94	0.00	0.79	0.00
E10.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	18.72	0.00	0.00	0.00	0.00	0.00	0.43	0.00
E10.Sp	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.00	9.72	0.24	0.00	0.00	0.27	0.00	0.12	0.00
E10.Su	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	3.45	0.08	0.00	0.00	0.63	0.00	0.16	0.00
E12.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E12.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	26.27	0.00	0.00	0.00	0.00
E12.Sp	0.00	0.20	0.00	0.86	0.00	0.00	0.00	0.00	0.00	10.22	0.00	0.00	0.98	0.00	0.00	0.04	0.00
E12.Su	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	5.45	0.33	0.00	0.00	0.00	0.00	0.00	0.00
E13.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E13.Wi	0.00	0.00	0.09	20.03	0.00	0.00	0.00	0.00	0.00	3.02	0.17	0.00	0.00	0.00	0.00	0.00	0.09
E13.Sp	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	7.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E13.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Au	0.00	0.00	0.00	0.46	0.46	0.00	0.00	0.00	0.00	2.53	3.69	0.00	0.00	0.00	0.00	0.00	0.00
E14.Wi	0.00	0.00	0.00	0.77	0.65	0.00	0.00	0.00	0.39	0.90	0.71	0.13	0.00	0.13	0.00	0.00	0.00
E14.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	7.96	6.67	0.00	0.00	0.00	0.00	0.00	0.00
E14.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Au	0.00	0.00	0.00	0.00	38.43	0.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.41	0.00	0.00	0.00
E15.Wi	0.00	0.00	0.00	16.07	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.31	0.00	0.00	0.00	0.00
E15.Sp	0.00	0.00	0.00	6.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E16.Au	0.00	0.00	0.00	0.00	23.10	0.00	0.00	0.00	0.00	0.00	0.66	0.00	3.96	0.33	0.00	0.00	0.00
E16.Wi	0.00	0.00	0.09	2.49	0.00	0.00	0.00	0.31	0.00	3.72	1.92	0.00	0.00	0.00	0.00	0.00	0.00
E16.Sp	0.00	0.00	0.00	0.56	0.00	0.00	0.00	0.00	0.00	2.42	0.00	0.00	0.00	1.13	0.00	0.00	0.00
E16.Su	0.00	0.00	0.34	0.00	0.00	0.00	0.00	0.00	0.00	3.92	0.00	0.00	0.00	0.00	0.00	0.00	0.00

(continuation)

Code	TriChi	TriCru	TriCyr	TriEcn	TriFHyd	TriFLim	TriFPhi	TriFPol	TriHol	TriHyd	TriHydp	TriHypr	TriLimn	TriMes	TriMys	TriOrt	TriOxy
A1.Au	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.25	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.31
A1.Wi	0.00	0.00	0.00	0.00	0.73	0.00	0.00	0.00	0.00	1.09	0.46	0.00	0.00	0.00	0.00	0.00	0.18
A1.Sp	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.00	1.72	0.47	0.00	0.00	0.00	0.00	0.00	0.00
A1.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Wi	0.00	0.00	0.25	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00
A2.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A3.Au	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.00	0.13	0.26
A3.Wi	0.00	0.12	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.08	2.65	0.00	0.24	0.00	0.00	0.00	0.00
A3.Sp	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.43	0.00	0.00	0.69	0.00	0.00	0.00	0.00	0.00	0.00
A3.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A4.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.64	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00
A4.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.06	0.00	0.00
A4.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	1.24	4.52	0.68	0.13	0.00	0.00	0.00	0.00	0.43
A4.Su	1.52	0.00	0.00	0.36	0.00	0.00	0.00	0.00	0.09	0.00	1.17	0.00	0.00	0.00	0.00	0.54	0.18
A5.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A5.Wi	0.00	0.00	0.00	0.00	0.03	0.11	0.00	0.00	0.00	0.80	0.00	0.00	0.00	0.01	0.00	0.00	0.00
A5.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.06	0.19	0.00	0.00	0.00	0.00	0.00	0.00
A5.Su	0.23	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.23	6.31	0.00	0.00	0.00	0.00	0.00	0.00
A6.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A6.Wi	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.29	0.00	0.00	0.00
A6.Sp	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.34	0.17	0.00	0.00	0.00	0.00	0.00
A6.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Au	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Wi	0.00	0.00	0.00	0.00	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.44	0.00	0.00	0.00
A7.Sp	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.23	0.00	0.00	0.00	0.00	0.00	0.00
A7.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00
A8.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Su	0.00	0.00	0.00	1.19	0.00	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

(continuation)

Code	TriChi	TriCru	TriCyr	TriEcn	TriFHyd	TriFLim	TriFPhi	TriFPol	TriHol	TriHyd	TriHydp	TriHypr	TriLimn	TriMes	TriMys	TriOrt	TriOxy
A9.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Wi	0.00	0.00	0.00	0.00	0.00	0.68	0.00	0.00	0.00	0.00	0.34	0.00	0.00	0.00	0.00	0.00	0.00
A9.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E10.Au	0.00	0.00	0.00	0.00	0.00	0.79	0.00	0.00	0.00	0.00	0.79	0.00	0.00	0.00	0.00	0.00	0.00
E10.Wi	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.34	0.00	0.00	0.00	0.00	0.00	0.00	0.17
E10.Sp	0.00	0.00	0.00	0.00	0.09	0.03	0.00	0.03	0.00	5.68	0.03	0.00	0.00	0.00	0.00	0.00	4.13
E10.Su	0.00	0.00	0.00	0.00	0.24	0.00	0.00	0.31	0.00	0.24	0.31	0.00	0.00	0.00	0.00	0.00	0.63
E12.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E12.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.45
E12.Sp	0.00	0.00	0.00	0.00	2.00	0.04	0.00	0.00	0.00	0.00	0.41	0.00	0.00	0.00	0.00	0.08	1.18
E12.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.33
E13.Au	0.00	0.00	0.00	0.00	0.00	1.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E13.Wi	0.00	0.00	0.00	0.00	0.00	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E13.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.07
E13.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Au	0.00	0.00	0.00	0.00	0.00	0.23	0.00	0.00	0.00	0.00	0.23	0.00	0.00	0.00	0.00	0.00	0.00
E14.Wi	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.26	0.00	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.19
E14.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	3.44	1.40	0.00	0.00	0.00	0.00	0.00	2.26
E14.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Au	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E16.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E16.Wi	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	1.57	0.22	0.00	0.00	0.00	0.26	0.00	0.04
E16.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16	4.35	0.00	0.00	0.00	0.00	0.00	0.24
E16.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

(continuation)

Code	TriPar	TriPle	TriPol	TriPse	TriRhy	TriRya	TriSch	TriSl	TriSta	TriTin	TriWor
A1.Au	0.00	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A1.Wi	0.00	0.27	0.00	0.00	0.00	0.00	0.00	8.74	0.00	0.00	0.00
A1.Sp	0.00	0.00	0.00	0.00	0.16	0.00	0.00	1.25	0.00	0.00	0.00
A1.Su	0.00	0.00	0.73	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00
A2.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A2.Su	0.00	0.00	0.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A3.Au	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A3.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.81	0.00
A3.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.34	0.00	0.26	0.00
A3.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.75	0.00
A4.Au	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A4.Wi	0.00	0.12	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.72	0.00
A4.Sp	0.09	0.00	0.51	0.00	0.00	0.00	0.00	2.39	0.00	0.26	0.00
A4.Su	0.00	0.00	1.08	0.00	0.00	0.00	0.00	0.09	0.00	0.18	0.00
A5.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00
A5.Wi	0.00	0.01	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
A5.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.95	0.00	0.00	0.00
A5.Su	0.00	0.00	0.53	0.00	0.00	0.00	0.00	1.35	0.00	0.08	0.00
A6.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A6.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.43	0.00	0.29	0.00
A6.Sp	0.17	0.00	0.00	0.00	0.00	0.00	0.00	1.51	0.00	3.02	0.00
A6.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.31	0.00
A7.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A7.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.09	0.00
A7.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.34	0.00
A8.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A8.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

(continuation)

Code	TriPar	TriPle	TriPol	TriPse	TriRhy	TriRya	TriSch	TriSl	TriSta	TriTin	TriWor
A9.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Wi	0.00	0.00	0.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A9.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E10.Au	0.00	1.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E10.Wi	0.00	1.02	5.02	0.00	0.00	0.00	0.34	0.00	0.00	1.19	0.00
E10.Sp	0.00	0.00	1.09	0.00	0.00	0.00	0.00	1.34	0.00	1.15	0.00
E10.Su	0.00	0.00	1.88	0.00	0.00	0.00	0.00	0.39	0.00	0.94	0.00
E12.Au	0.00	1.37	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E12.Wi	0.00	0.00	1.64	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E12.Sp	0.00	0.00	2.08	0.00	0.00	0.00	0.00	0.53	0.00	0.04	0.00
E12.Su	0.00	0.00	3.64	0.00	0.00	0.00	0.00	1.32	0.00	0.00	0.00
E13.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.69	0.00
E13.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.35	0.00
E13.Sp	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.00
E13.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Au	0.00	0.00	0.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E14.Wi	0.00	0.19	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.58	0.00
E14.Sp	0.00	0.00	0.32	0.00	0.00	0.00	0.00	0.75	0.11	0.00	0.00
E14.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Au	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Wi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E15.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E16.Au	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00
E16.Wi	0.13	0.00	0.26	0.00	0.00	0.35	0.00	0.00	0.00	0.00	0.00
E16.Sp	0.81	0.24	0.64	0.16	0.00	0.00	0.00	0.48	0.00	0.24	0.40
E16.Su	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table S1.4. Codes used to refer to different taxa.

Order	Family	Genus	species	Code
Amphipoda	Gammaridae	Echinogammarus		AmpEch
Amphipoda	Gammaridae	Gammarus		AmpGam
Annelida	Hirudinea			AnnHir
Annelida	Oligochaeta			AnnOli
Sphaeriida	Sphaeriidae	Pisidium		BivPis
Coleoptera	Dryopidae	Dryops		ColDry
Coleoptera	Dysticidae	Agabus		ColAga
Coleoptera	Dysticidae	Bidessus		ColBid
Coleoptera	Dysticidae	Deronectes		ColDer
Coleoptera	Dysticidae	Graptodytes		ColGra
Coleoptera	Dysticidae	Hydroglyphus		ColHydg
Coleoptera	Dysticidae	Hydroporus		ColHyd
Coleoptera	Dysticidae	Hydrovatus		ColHydv
Coleoptera	Dysticidae	Ilybius		ColIly
Coleoptera	Dysticidae	Melademа	coriacea	ColMel
Coleoptera	Dysticidae	Nebrioporus		ColNeb
Coleoptera	Dysticidae	sF.Hydroporinae		ColHydo
Coleoptera	Dysticidae	Stictonectes		ColSti
Coleoptera	Dysticidae	Yola	bicarinata	ColYol
Coleoptera	Dysticidae			ColDys
Coleoptera	Elmidae	Elmis		ColElm
Coleoptera	Elmidae	Esolus		ColEso
Coleoptera	Elmidae	Haliplus		ColHal
Coleoptera	Elmidae	Limnius		ColLim
Coleoptera	Elmidae	Oulimnius		ColOul
Coleoptera	Elmidae	Riolus		ColRio
Coleoptera	Elmidae	Stenelmis	canaliculata	ColSte
Coleoptera	Elmidae			ColFElm
Coleoptera	Gyrinidae	Gyrinus		ColGyr
Coleoptera	Gyrinidae	Orectochilus	villosus	ColOre
Coleoptera	Haliplidae	Peltodytes		ColPel
Coleoptera	Haliplidae			ColFHal
Coleoptera	Hydraenidae	Helophorus		ColHelp
Coleoptera	Hydraenidae	Hydraena		ColHydr
Coleoptera	Hydraenidae	Ochthebius		ColOch
Coleoptera	Hydrophilidae	Berosus		ColBer
Coleoptera	Hydrophilidae	Coelostoma		ColCoe
Coleoptera	Hydrophilidae	Helochares	lividus	ColHel
Coleoptera	Hydrophilidae	Laccobius		ColLac

TABLE S1.4

(continuation)

Order	Family	Genus	species	Code
Coleoptera	Hydrophilidae			ColFHyd
Coleoptera	Hygrobiidae	Hygrobia	hermanni	ColHyg
Coleoptera	Scirtidae	Cyphon		ColCyp
Coleoptera	Scirtidae	Hydrocyphon		ColHydc
Coleoptera	Scirtidae	Scirtes		ColSci
Coleoptera	Scirtidae			ColFSci
Decapoda	Cambaridae	Procambarus	clarkii	DecPro
Decapoda	Cambaridae			DecCam
Decapoda	Hippolytidae	Atyaephyra	desmarestiiÿ	DecAty
Diptera	Athericidae	Atherix		DipAth
Diptera	Athericidae	Atrichops	crassipes	DipAtr
Diptera	Athericidae			DipFAth
Diptera	Ceratopogonidae	sF.Ceratopogoninae		DipCera
Diptera	Ceratopogonidae	sF.Dasyheleinae		DipDasy
Diptera	Ceratopogonidae	sF.Forcipomyiinae		DipFor
Diptera	Ceratopogonidae			DipCer
Diptera	Chironomidae	sF.Orthocladiinae		DipOrth
Diptera	Chironomidae	sF.Prodiamesinae		DipProd
Diptera	Chironomidae	sF.Tanypodinae		DipTany
Diptera	Chironomidae	sT.Chironomini		DipChirn
Diptera	Chironomidae	Tr.Tanytarsini		DipTant
Diptera	Culicidae	Anopheles		DipAno
Diptera	Culicidae	sF.Culicinae		DipCuli
Diptera	Dixidae	Dixa		DipDixa
Diptera	Dixidae	Dixella		DipDix
Diptera	Dixidae			DipFDix
Diptera	Dolichopodidae			DipDol
Diptera	Empididae	sF.Clinocerinae		DipClin
Diptera	Empididae	sF.Hemerodromiinae		DipHem
Diptera	Limoniidae	Tr.Eriopterini		DipEri
Diptera	Limoniidae	Tr.Hexatomini		DipHex
Diptera	Limoniidae			DipFLim
Diptera	Psychodidae			DipPsy
Diptera	Ptychopteridae			DipPty
Diptera	Rhagionidae			DipRha
Diptera	Sciomyzidae			DipSci
Diptera	Simuliidae	Tr.Prosimuliini		DipPro
Diptera	Simuliidae	Tr.Simuliini		DipSim
Diptera	Simuliidae			DipFSim

Order	Family	Genus	species	Code
Diptera	Stratiomyidae			DipStr
Diptera	Syrphidae			DipSyr
Diptera	Tabanidae			DipTab
Diptera	Tipulidae	Tr.Limoniini		DipLim
Diptera	Tipulidae	Tr.Pediciini		DipPed
Diptera	Tipulidae			DipTip
Ephemera	Baetidae	Acentrella		EphAce
Ephemera	Baetidae	Baetis		EphBae
Ephemera	Baetidae	Centroptilum		EphCen
Ephemera	Baetidae	Cloeon		EphClo
Ephemera	Baetidae	Procloeon		EphPro
Ephemera	Baetidae			EphFBae
Ephemera	Caenidae	Caenis		EphCae
Ephemera	Ephemerellidae	Ephemerella	sensu lato	EphEphl
Ephemera	Heptageniidae	Ecdyonurus		EphEcd
Ephemera	Heptageniidae	Heptagenia		EphHep
Ephemera	Heptageniidae			EphFHep
Ephemera	Leptophebiidae	Thraulus	bellus	EphThr
Ephemera	Leptophebiidae			EphLep
Ephemera	Leptophlebiidae	Choroterpes	picteti	EphCho
Ephemera	Leptophlebiidae	Habroleptoides		EphHabp
Ephemera	Leptophlebiidae	Habrophlebia		EphHab
Ephemera	Leptophlebiidae	Paraleptophlebia		EphPar
Gastropoda	Ancylidae			GasFAnc
Gastropoda	Bithyniidae	Bithynia		GasBit
Gastropoda	Bythinellidae	Bythinella		GasByt
Gastropoda	Bythinellidae			GasFByt
Gastropoda	Hydrobiidae	Bythiospeum		GasByts
Gastropoda	Hydrobiidae			GasHyd
Gastropoda	Lymnaeidae	Galba		GasGal
Gastropoda	Lymnaeidae	Radix		GasRad
Gastropoda	Lymnaeidae			GasLym
Gastropoda	Physidae	Physa		GasPhy
Gastropoda	Physidae	Physella		GasPhyl
Gastropoda	Physidae			GasFPhy
Gastropoda	Planorbidae	Ancylus		GasAnc
Gastropoda	Tateidae	Potamopyrgus		GasPot
Gastropoda	Valvatidae	Valvata		GasVal
Hemiptera	Corixidae	Arctocorisa		HemArc
Hemiptera	Corixidae	Micronecta		HemMict

TABLE S1.4

(continuation)

Order	Family	Genus	species	Code
Hemiptera	Corixidae			HemCor
Hemiptera	Gerridae	Aquarius		HemAqu
Hemiptera	Gerridae	Gerris		HemGer
Hemiptera	Hydrometridae	Hydrometra		HemHyd
Hemiptera	Naucoridae	Naucoris	maculatus	HemNau
Hemiptera	Notonectidae	Notonecta		HemNot
Hemiptera	Pleidae	Plea		HemPle
Hemiptera	Veliidae	Microvelia		HemMic
Hemiptera	Veliidae	Velia		HemVel
Megaloptera	Sialidae	Sialis		MegSia
Nematomorpha				Nem
Odonata	Aeshnidae	Aeshna		OdoAes
Odonata	Aeshnidae	Anax		OdoAna
Odonata	Aeshnidae	Boyeria	irene	OdoBoy
Odonata	Calopterygidae	Calopteryx		OdoCal
Odonata	Coenagrionidae	Coenagrion		OdoCoe
Odonata	Coenagrionidae			OdoFCoe
Odonata	Cordulegasteridae	Cordulegaster	boltonii	OdoCor
Odonata	Corduliidae	Macromia	splendens	OdoMac
Odonata	Corduliidae	Oxygastra	curtisii	OdoOxy
Odonata	Corduliidae			OdoFCor
Odonata	Gomphidae	Gomphus		OdoGom
Odonata	Gomphidae	Onychogomphus		OdoOny
Odonata	Gomphidae			OdoFGom
Odonata	Lestidae	Lestes		OdoLes
Odonata	Lestidae	Sympecma	fusca	OdoSymf
Odonata	Lestidae			OdoFLes
Odonata	Libellulidae	Orthetrum		OdoOrt
Odonata	Libellulidae	Sympetrum		OdoSym
Odonata	Libellulidae			OdoLib
Odonata	Platycnemididae	Platycnemis		OdoPla
Odonata	sO.Anisoptera			OdosAno
Odonata	sO.Zygoptera			OdosZyg
Odonata		SI		OdoSI
Plecoptera	Capniidae	Capnia		PleCap
Plecoptera	Capniidae	Capnioneura		PleCapn
Plecoptera	Capniidae			PleFCap
Plecoptera	Leuctridae	Leuctra		PleLeu
Plecoptera	Nemouridae	Nemoura		PleNem

Order	Family	Genus	species	Code
Plecoptera	Perlodidae	Hemimelaena	flaviventris	PleHem
Plecoptera	Perlodidae	Isoperla		PleIso
Plecoptera	Perlodidae	Perlodes		PlePer
Plecoptera	Perlodidae			PleFPer
Plecoptera		SI		PleSI
Trichoptera	Calamoceratidae	Calamoceras		TriCal
Trichoptera	Ecnomidae	Ecnomus		TriEcn
Trichoptera	Hydropsychidae	Cheumatopsyche		TriChe
Trichoptera	Hydropsychidae	Hydropsyche		TriHydp
Trichoptera	Hydroptilidae	Agraylea		TriAgr
Trichoptera	Hydroptilidae	Hydroptila		TriHyd
Trichoptera	Hydroptilidae	Orthotrichia		TriOrt
Trichoptera	Hydroptilidae	Oxyethira		TriOxy
Trichoptera	Hydroptilidae	Stactobia		TriSta
Trichoptera	Hydroptilidae			TriFHyd
Trichoptera	Lepidostomatidae	Crunoecia		TriCru
Trichoptera	Leptoceridade	Mystacides		TriMys
Trichoptera	Limnephilidae	Mesophylax		TriMes
Trichoptera	Limnephilidae	sF.Limnephilinae		TriLimn
Trichoptera	Limnephilidae			TriFLim
Trichoptera	Philopotamidae	Chimarra		TriChi
Trichoptera	Philopotamidae	Wormaldia		TriWor
Trichoptera	Philopotamidae			TriFPhi
Trichoptera	Polycentropodidae	Cyrnus		TriCyr
Trichoptera	Polycentropodidae	Holocentropus		TriHol
Trichoptera	Polycentropodidae	Plectrocnemia		TriPle
Trichoptera	Polycentropodidae	Polycentropus		TriPol
Trichoptera	Polycentropodidae	Pseudoneureclipsis	lusitanicus	TriPse
Trichoptera	Polycentropodidae			TriFPol
Trichoptera	Psychomyiidae	Tinodes		TriTin
Trichoptera	Rhyacophilidae	Hyporhyacophila		TriHypr
Trichoptera	Rhyacophilidae	Pararhyacophila		TriPar
Trichoptera	Rhyacophilidae	Ryacophila		TriRya
Trichoptera	Rhyacophilidae			TriRhy
Trichoptera	Sericostomatidae	Schizopelex		TriSch
Trichoptera		SI		TriSI
Tricladia				Tri

Table S1.5. Taxonomic and functional alpha diversity metrics. The codes correspond to those in Table S1.2. Abbreviations include S (taxon richness), H' (diversity index), FRic (functional richness), and FRed (functional redundancy).

Code	Reach	Season	S	H	EPT	FRic	FRed
A1.Au	A1	Au	29	1.54	0.41	0.34	0.43
A1.Sp	A1	Sp	23	1.55	0.58	0.28	0.48
A1.Su	A1	Su	31	2.35	0.48	0.34	0.45
A1.Wi	A1	Wi	24	1.52	0.32	0.28	0.57
A2.Au	A2	Au	24	2.01	0.33	0.28	0.42
A2.Sp	A2	Sp	17	2.34	0.42	0.28	0.45
A2.Su	A2	Su	14	0.99	0.24	0.28	0.43
A2.Wi	A2	Wi	31	1.78	0.43	0.34	0.42
A3.Au	A3	Au	48	2.08	0.40	0.46	0.44
A3.Sp	A3	Sp	39	2.13	0.42	0.46	0.48
A3.Su	A3	Su	20	2.14	0.28	0.28	0.40
A3.Wi	A3	Wi	33	2.05	0.20	0.41	0.47
A4.Au	A4	Au	44	1.77	0.32	0.46	0.40
A4.Sp	A4	Sp	46	2.89	0.35	0.46	0.44
A4.Su	A4	Su	41	2.80	0.39	0.46	0.39
A4.Wi	A4	Wi	46	2.17	0.34	0.46	0.42
A5.Au	A5	Au	27	0.88	0.22	0.34	0.40
A5.Sp	A5	Sp	40	2.58	0.46	0.46	0.41
A5.Su	A5	Su	40	2.78	0.30	0.46	0.42
A5.Wi	A5	Wi	39	1.59	0.35	0.46	0.43
A6.Au	A6	Au	20	1.07	0.25	0.28	0.37
A6.Sp	A6	Sp	30	2.39	0.47	0.34	0.46
A6.Su	A6	Su	9	1.04	0.37	0.25	0.27
A6.Wi	A6	Wi	32	2.00	0.33	0.41	0.44
A7.Au	A7	Au	19	1.22	0.26	0.28	0.38
A7.Sp	A7	Sp	34	1.67	0.46	0.41	0.42
A7.Wi	A7	Wi	28	1.89	0.32	0.34	0.43
A8.Au	A8	Au	17	0.78	0.35	0.28	0.41
A8.Sp	A8	Sp	7	1.56	0.43	0.19	0.49
A8.Su	A8	Su	21	1.71	0.29	0.28	0.40
A8.Wi	A8	Wi	21	1.88	0.29	0.28	0.45
A9.Au	A9	Au	17	1.32	0.24	0.28	0.42
A9.Sp	A9	Sp	17	1.36	0.38	0.28	0.47
A9.Su	A9	Su	8	0.66	0.29	0.25	0.41
A9.Wi	A9	Wi	24	2.28	0.25	0.28	0.48
E10.Au	E10	Au	26	2.89	0.35	0.34	0.45
E10.Sp	E10	Sp	53	2.86	0.35	0.59	0.49

(continuation)

Code	Reach	Season	S	H	EPT	FRic	FRed
E10.Su	E10	Su	49	2.90	0.42	0.58	0.41
E10.Wi	E10	Wi	46	3.01	0.41	0.46	0.48
E12.Au	E12	Au	14	1.86	0.36	0.28	0.49
E12.Sp	E12	Sp	55	2.22	0.38	0.65	0.47
E12.Su	E12	Su	27	2.15	0.35	0.34	0.53
E12.Wi	E12	Wi	21	1.72	0.37	0.28	0.50
E13.Au	E13	Au	29	2.36	0.17	0.34	0.40
E13.Sp	E13	Sp	29	1.41	0.33	0.34	0.44
E13.Wi	E13	Wi	27	1.69	0.31	0.34	0.41
E14.Au	E14	Au	25	2.00	0.48	0.28	0.37
E14.Sp	E14	Sp	48	2.82	0.50	0.46	0.46
E14.Wi	E14	Wi	42	2.37	0.38	0.46	0.47
E15.Au	E15	Au	16	1.24	0.44	0.28	0.34
E15.Sp	E15	Sp	19	1.88	0.27	0.28	0.33
E15.Wi	E15	Wi	26	2.19	0.21	0.34	0.37
E16.Au	E16	Au	35	2.37	0.31	0.46	0.40
E16.Sp	E16	Sp	39	2.55	0.42	0.46	0.46
E16.Su	E16	Su	28	2.03	0.49	0.34	0.42
E16.Wi	E16	Wi	43	2.65	0.25	0.46	0.50

Table S1.6. Taxonomic and functional β diversity metrics. Abbreviations: TβD (taxonomic beta diversity), TβRepl (taxonomic species replacement component), TβRich (taxonomic richness difference component), FβD (functional beta diversity), FβRepl (functional species replacement component), and FβRich (functional richness difference component).

Reach	TβD	TβRepl	TβRich	FβD	FβRepl	FβRich
A1	0.28	0.23	0.04	0.18	0.18	0.00
A2	0.30	0.19	0.11	0.23	0.23	0.00
A3	0.28	0.17	0.11	0.17	0.17	0.00
A4	0.26	0.24	0.02	0.21	0.21	0.00
A5	0.25	0.20	0.05	0.24	0.24	0.00
A6	0.31	0.14	0.16	0.26	0.26	0.00
A7	0.39	0.10	0.30	0.58	0.08	0.50
A8	0.29	0.15	0.14	0.24	0.24	0.00
A9	0.30	0.17	0.13	0.47	0.47	0.00
E10	0.19	0.10	0.09	0.14	0.14	0.00
E12	0.30	0.13	0.17	0.27	0.27	0.00
E13	0.37	0.12	0.26	0.58	0.08	0.50
E14	0.36	0.06	0.30	0.59	0.09	0.50

TABLE S1.6

Reach	TβD	TβRepl	TβRich	FβD	FβRepl	FβRich
E15	0.41	0.12	0.29	0.69	0.19	0.50
E16	0.27	0.22	0.06	0.22	0.22	0.00

Table S1.7. Generalized linear latent variable model (GLLVM) built with a zero-inflated Poisson distribution, log-link function, and one latent variable. The predictor abbreviations used were DD (dry-phase duration), Season.Au (autumn sampling campaign), Season.Wi (winter sampling campaign), Season.Sp (spring sampling campaign), and Season.Su (summer sampling campaign).

Family: ZIP

AIC: 3111.063 **AICc:** 3434.842 **BIC:** 9720.75

LL: -586.5 **df**: 969

Informed LVs: 0

Constrained LVs: 0

Unconstrained LVs: 1

Formula: ~season + DIN + DD

LV formula: ~yNULL

Coefficients predictors (only significant predictors):

Predictor	Sp code	Estimate	Std.error	z-value	Pr(→|z|)
DD	OdoLib	-1.85E+01	3.88E+00	-4.76E+00	1.91E-06
DD	BivPis	-1.67E+01	3.32E+00	-5.02E+00	5.30E-07
DD	DipClin	-1.59E+01	2.28E+00	-6.96E+00	3.41E-12
DD	TriHol	-1.44E+01	1.76E+00	-8.16E+00	3.27E-16
DD	DipAtr	-1.43E+01	1.30E+00	-1.10E+01	2.00E-16
DD	MegSia	-1.24E+01	1.29E+00	-9.58E+00	2.00E-16
DD	TriChi	-1.25E+01	1.06E+00	-1.18E+01	2.00E-16
Season.Wi	MegSia	1.14E+01	5.75E+00	1.99E+00	0.046666
Season.Wi	GasGal	1.39E+01	4.18E+00	3.33E+00	0.000878
Season.Wi	HemGer	1.43E+01	3.96E+00	3.61E+00	0.000306
Season.Wi	ColNeb	1.23E+01	3.31E+00	3.72E+00	0.0002
Season.Wi	DipAtr	1.43E+01	3.75E+00	3.80E+00	0.000146
Season.Wi	ColLac	1.50E+01	3.62E+00	4.14E+00	3.45E-05
Season.Wi	OdosZyg	1.43E+01	3.19E+00	4.48E+00	7.49E-06
Season.Wi	TriMes	1.80E+01	3.63E+00	4.95E+00	7.43E-07
Season.Wi	OdoLes	1.62E+01	3.07E+00	5.28E+00	1.28E-07
Season.Wi	TriFHyd	1.59E+01	2.75E+00	5.78E+00	7.61E-09
Season.Wi	HemMic	1.65E+01	2.71E+00	6.11E+00	1.01E-09
Season.Wi	DipDix	1.84E+01	2.74E+00	6.69E+00	2.17E-11
Season.Wi	ColSti	1.74E+01	2.43E+00	7.17E+00	7.54E-13
Season.Wi	PlePer	1.61E+01	2.23E+00	7.20E+00	6.03E-13
Season.Wi	OdoSl	1.69E+01	2.20E+00	7.65E+00	2.03E-14
Season.Wi	ColDry	-2.04E+01	7.17E-07	-2.84E+07	2.00E-16
Season.Wi	ColFHyd	-9.55E+00	5.96E-07	-1.60E+07	2.00E-16

TABLE S1.7
(continuation)

Predictor	Sp code	Estimate	Std.error	z-value	Pr(→|z|)
Season.Wi	ColHyd	2.29E+01	1.59E+00	1.45E+01	2.00E-16
Season.Wi	ColHydg	2.81E+01	2.29E+00	1.23E+01	2.00E-16
Season.Wi	DecAty	-1.09E+01	3.14E-08	-3.46E+08	2.00E-16
Season.Wi	DipCer	-1.21E+01	7.01E-05	-1.73E+05	2.00E-16
Season.Wi	DipPed	-1.00E+01	7.53E-05	-1.33E+05	2.00E-16
Season.Wi	DipProd	-8.67E+00	1.19E-07	-7.26E+07	2.00E-16
Season.Wi	EphCho	-7.39E+00	2.62E-08	-2.82E+08	2.00E-16
Season.Wi	GasByts	-1.15E+01	6.51E-03	-1.76E+03	2.00E-16
Season.Wi	GasFAnc	2.44E+01	9.51E-01	2.56E+01	2.00E-16
Season.Wi	HemNot	2.38E+01	1.91E+00	1.25E+01	2.00E-16
Season.Wi	OdoFCoe	-2.30E+01	7.13E-09	-3.23E+09	2.00E-16
Season.Wi	OdoFCor	1.93E+01	1.79E+00	1.08E+01	2.00E-16
Season.Wi	OdoFLes	-6.41E+00	6.65E-09	-9.64E+08	2.00E-16
Season.Wi	OdoLib	-1.28E+01	8.24E-05	-1.55E+05	2.00E-16
Season.Wi	PleHem	2.11E+01	1.37E+00	1.55E+01	2.00E-16
Season.Wi	PleIso	1.93E+01	1.61E+00	1.20E+01	2.00E-16
Season.Wi	TriChi	-1.18E+01	1.72E-13	-6.89E+13	2.00E-16
Season.Wi	TriEcn	-7.49E+00	7.08E-13	-1.06E+13	2.00E-16
Season.Wi	TriHol	-2.11E+01	1.02E-07	-2.08E+08	2.00E-16
Season.Wi	TriHyd	2.10E+01	1.30E+00	1.61E+01	2.00E-16
Season.Wi	TriOrt	-1.71E+01	1.77E-06	-9.67E+06	2.00E-16
Season.Wi	TriSI	2.07E+01	1.34E+00	1.54E+01	2.00E-16
Season.Su	EphCho	1.94E+01	9.34E+00	2.08E+00	0.037394
Season.Su	DecAty	1.81E+01	7.03E+00	2.57E+00	0.010145
Season.Su	OdoLes	1.54E+01	4.33E+00	3.56E+00	0.000377
Season.Su	DipDix	1.67E+01	4.35E+00	3.85E+00	0.000118
Season.Su	MegSia	1.39E+01	3.48E+00	4.00E+00	6.47E-05
Season.Su	ColSti	1.63E+01	3.93E+00	4.14E+00	3.45E-05
Season.Su	TriFHyd	1.56E+01	3.59E+00	4.34E+00	1.42E-05
Season.Su	HemGer	1.52E+01	3.36E+00	4.52E+00	6.08E-06
Season.Su	ColLac	1.57E+01	3.28E+00	4.79E+00	1.68E-06
Season.Su	OdosZyg	1.50E+01	3.00E+00	5.02E+00	5.27E-07
Season.Su	AmpEch	1.50E+01	2.67E+00	5.64E+00	1.67E-08
Season.Su	DipAtr	1.66E+01	2.80E+00	5.93E+00	3.04E-09
Season.Su	DipProd	1.78E+01	2.96E+00	6.00E+00	1.97E-09
Season.Su	HemMic	1.75E+01	2.33E+00	7.50E+00	6.29E-14
Season.Su	AnnHir	-1.81E+01	2.16E-06	-8.38E+06	2.00E-16
Season.Su	ColAga	-1.19E+01	7.49E-05	-1.59E+05	2.00E-16
Season.Su	ColDer	-6.23E+01	2.03E-06	-3.08E+07	2.00E-16
Season.Su	ColDys	-1.35E+01	1.66E-05	-8.14E+05	2.00E-16

(continuation)

Predictor	Sp code	Estimate	Std.error	z-value	Pr(→|z|)
Season.Su	ColFHyd	-8.09E+00	1.98E-05	-4.10E+05	2.00E-16
Season.Su	ColHal	-1.90E+01	6.43E-08	-2.95E+08	2.00E-16
Season.Su	ColHyd	-1.01E+01	3.01E-07	-3.34E+07	2.00E-16
Season.Su	ColHydg	-7.83E+00	5.66E-07	-1.38E+07	2.00E-16
Season.Su	ColNeb	-1.19E+01	2.39E-07	-4.97E+07	2.00E-16
Season.Su	ColOch	-1.88E+01	1.23E-06	-1.53E+07	2.00E-16
Season.Su	DipClin	-1.15E+01	7.36E-05	-1.57E+05	2.00E-16
Season.Su	DipFLim	-1.53E+01	1.70E-06	-9.04E+06	2.00E-16
Season.Su	DipPed	-6.88E+00	6.32E-04	-1.09E+04	2.00E-16
Season.Su	DipPro	-1.34E+01	2.17E-05	-6.20E+05	2.00E-16
Season.Su	DipRha	-1.14E+01	1.45E-02	-7.88E+02	2.00E-16
Season.Su	EphEcd	-2.12E+01	1.06E-07	-1.99E+08	2.00E-16
Season.Su	GasBit	-1.93E+01	1.18E-07	-1.63E+08	2.00E-16
Season.Su	GasFAnc	-7.91E+00	5.09E-09	-1.55E+09	2.00E-16
Season.Su	GasGal	1.81E+01	1.70E+00	1.06E+01	2.00E-16
Season.Su	GasHyd	-1.82E+01	8.21E-08	-2.21E+08	2.00E-16
Season.Su	GasLym	-1.53E+01	2.03E-06	-7.51E+06	2.00E-16
Season.Su	GasPhyl	-2.40E+01	1.20E-08	-2.00E+09	2.00E-16
Season.Su	GasPot	-7.76E+00	7.22E-04	-1.07E+04	2.00E-16
Season.Su	HemNot	-1.01E+01	5.36E-09	-1.89E+09	2.00E-16
Season.Su	OdoFCor	-7.72E+00	8.68E-09	-8.90E+08	2.00E-16
Season.Su	OdoFLes	-8.44E+00	8.40E-09	-1.01E+09	2.00E-16
Season.Su	OdoOxy	-2.26E+01	2.44E-08	-9.26E+08	2.00E-16
Season.Su	OdoSI	1.76E+01	2.04E+00	8.62E+00	2.00E-16
Season.Su	PleCapn	-2.64E+01	6.04E-09	-4.38E+09	2.00E-16
Season.Su	PleHem	-1.04E+01	2.25E-09	-4.59E+09	2.00E-16
Season.Su	PleIso	-6.46E+00	7.56E-09	-8.54E+08	2.00E-16
Season.Su	PlePer	-1.02E+01	8.25E-11	-1.23E+11	2.00E-16
Season.Su	PleSI	-1.84E+01	6.76E-08	-2.72E+08	2.00E-16
Season.Su	TriChi	1.89E+01	1.43E+00	1.33E+01	2.00E-16
Season.Su	TriEcn	2.14E+01	1.39E+00	1.53E+01	2.00E-16
Season.Su	TriFLim	-2.05E+01	7.73E-09	-2.65E+09	2.00E-16
Season.Su	TriHyd	2.02E+01	1.96E+00	1.03E+01	2.00E-16
Season.Su	TriMes	-9.73E+00	1.86E-11	-5.24E+11	2.00E-16
Season.Su	TriPar	-1.06E+01	1.15E-03	-9.22E+03	2.00E-16
Season.Su	TriPle	-2.17E+01	2.08E-09	-1.04E+10	2.00E-16
Season.Su	TriSI	2.09E+01	1.45E+00	1.44E+01	2.00E-16
Season.Sp	OdosZyg	1.31E+01	4.65E+00	2.81E+00	0.004937
Season.Sp	MegSia	1.20E+01	4.23E+00	2.85E+00	0.004441

TABLE S1.7

(continuation)

Predictor	Sp code	Estimate	Std.error	z-value	Pr(→|z|)
Season.Sp	ColNeb	1.23E+01	3.68E+00	3.33E+00	0.000859
Season.Sp	PlePer	1.34E+01	3.90E+00	3.43E+00	0.000604
Season.Sp	OdoSl	1.48E+01	4.22E+00	3.52E+00	0.000437
Season.Sp	AmpEch	1.34E+01	2.93E+00	4.58E+00	4.69E-06
Season.Sp	DecAty	1.92E+01	3.81E+00	5.04E+00	4.76E-07
Season.Sp	HemGer	1.52E+01	2.85E+00	5.34E+00	9.32E-08
Season.Sp	DipDix	1.78E+01	3.05E+00	5.83E+00	5.69E-09
Season.Sp	OdoLes	1.66E+01	2.74E+00	6.05E+00	1.48E-09
Season.Sp	DipProd	1.79E+01	2.61E+00	6.85E+00	7.30E-12
Season.Sp	ColLac	1.64E+01	2.29E+00	7.14E+00	9.63E-13
Season.Sp	GasGal	1.61E+01	2.07E+00	7.78E+00	7.10E-15
Season.Sp	TriFHyd	1.67E+01	2.14E+00	7.82E+00	5.21E-15
Season.Sp	ColSti	1.77E+01	2.24E+00	7.91E+00	2.68E-15
Season.Sp	ColDry	-2.06E+01	1.74E-06	-1.18E+07	2.00E-16
Season.Sp	ColHyd	2.23E+01	1.92E+00	1.16E+01	2.00E-16
Season.Sp	ColHydg	-7.07E+00	5.08E-08	-1.39E+08	2.00E-16
Season.Sp	ColOch	-1.28E+01	1.56E-04	-8.20E+04	2.00E-16
Season.Sp	DipAtr	-1.17E+01	1.73E-07	-6.75E+07	2.00E-16
Season.Sp	EphCen	-2.12E+01	3.32E-08	-6.39E+08	2.00E-16
Season.Sp	EphCho	-8.21E+00	8.49E-08	-9.67E+07	2.00E-16
Season.Sp	EphLep	-2.51E+01	1.56E-07	-1.60E+08	2.00E-16
Season.Sp	GasBit	-2.01E+01	8.98E-08	-2.24E+08	2.00E-16
Season.Sp	GasFAnc	-7.86E+00	6.42E-08	-1.22E+08	2.00E-16
Season.Sp	GasLym	-1.68E+01	7.67E-07	-2.20E+07	2.00E-16
Season.Sp	GasPhyl	-2.29E+01	2.41E-08	-9.50E+08	2.00E-16
Season.Sp	HemMic	1.73E+01	2.09E+00	8.26E+00	2.00E-16
Season.Sp	HemNot	2.36E+01	2.06E+00	1.15E+01	2.00E-16
Season.Sp	OdoFCor	-8.62E+00	5.92E-09	-1.46E+09	2.00E-16
Season.Sp	OdoOny	-2.11E+01	7.17E-09	-2.95E+09	2.00E-16
Season.Sp	PleCapn	-2.69E+01	4.97E-09	-5.42E+09	2.00E-16
Season.Sp	PleHem	1.97E+01	1.97E+00	1.00E+01	2.00E-16
Season.Sp	PleIso	-7.86E+00	1.52E-09	-5.18E+09	2.00E-16
Season.Sp	TriChi	-1.09E+01	4.47E-13	-2.43E+13	2.00E-16
Season.Sp	TriEcn	-7.45E+00	9.44E-13	-7.89E+12	2.00E-16
Season.Sp	TriHyd	2.18E+01	1.09E+00	2.00E+01	2.00E-16
Season.Sp	TriMes	-9.64E+00	1.33E-11	-7.25E+11	2.00E-16
Season.Sp	TriSl	2.15E+01	1.04E+00	2.06E+01	2.00E-16

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Table S2.1. Study site description. Latitude (Lat N) and longitude (Long E) are provided in degrees. m a.s.l.: meters above sea level. Order: Strahler stream order. Dry-phase duration (days): total days without surface water during the study period. Pp (mm): total precipitation. Area (km2): stream basin size. Land cover (%): percentage of urban, agricultural, or naturally vegetated cover. Conductivity (µS/cm): water conductivity. OM (%): organic matter percentage of sediment dry weight. Porous size (mm): classification of dry sediment grains by size classes, according to the Wentworth scale. Water volume of the HZ sample (L): total volume of water pumped for hyporheic zone (HZ) samples.

Code	Stream	River Basin	Lat N	Long E	m.a.s.l.	Order	Sampling date (d/m/yyyy)	Dry-phase duration (days)	Pp (mm)	Area (km^2)	Land cover (%)		
											Urban	Agriculture	Natural
EB	Algars	Ebro	41º 2' 3.05"	0º 15' 7.24"	312	4	3/9/2020	16	388	96.8	0.01	57.57	42.41
FL	Riera de Joanetes	Fluvià	42º 7' 28.69"	2º 26' 27.30"	484	4	4/9/2020	57	1026	15.7	0	1.1	98.9
FO	El Foix	Foix	41º 23' 51.65"	1º 35' 36.94"	330	4	28/8/2020	64	590	26.9	0	100	0
LL	Riera de Talamanca	Llobregat	41º 44' 28.39"	1º 56' 9.94"	325	3	31/8/2020	69	732	10.9	2.2	0.9	96.9
TE	Riera de Sant Miquel	Ter	42º 6' 35.35"	2º 29' 19.30"	526	3	4/9/2020	52	963	13.3	0	0.6	99.4
TO	Riera de Montnegre	Tordera	41º 42' 33.62"	2º 32' 2.87"	110	3	28/8/2020	24	865	49.1	0	0.6	99.4

(continuation)

Code	Conductivity (µS/cm)	OM (%)	Grain size (µm) (Wenworth, 1922[1])							Water volume of the HZ sample (L)
			2000-5000 (Gravel)	1000-2000 (Very coarse sand)	500-1000 (Coarse sand)	250-500 (Medium Sand)	100-250 (Fine sand)	32-100 (Coarse silt)	←32 (Silt)	
EB	427.4 (± 58.7)	12.65	34.66	33.42	23.48	7.77	0.62	0.04	0.01	60
FL	266.0 (±22.4)	2.04	19.42	13.50	20.60	41.31	5.03	0.11	0.02	0
FO	713.7 (±97.6)	1.70	44.08	30.37	18.95	6.38	0.17	0.04	0.01	40
LL	330.6 (±22.4)	1.93	33.38	25.88	19.82	18.13	2.22	0.49	0.08	0
TE	492.7 (±19.4)	1.14	54.32	23.41	10.99	10.37	0.67	0.21	0.03	35
TO	306.8 (±25.6)	0.57	23.62	33.73	30.23	12.41	0.00	0.00	0.00	50

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Table S2.2. Taxa collected during sediment rehydration for each assemblage. Sample codes encompass stream initials and the replicate number. Taxon abbreviations can be found in Table S4. Here, (A) stands for the adult stage, and (L) signifies the larval stage. "Reh.Days", specific days during sediment rehydration. 'X', presence of 'Cop', copepods;'Daph', *Daphnia*; 'Ostr', ostracods.

Code	Days	EphProc	EphCaen	ColNebr	ColLimn	ColOuli	ColEsol	ColAgab	ColDryo	DipErio	DipChi	DipCera	DipTab	DipSci	DipStr	DipOrth	OdoGom	Nem	Oli	ProHyd	PulPhy	HirErp	Cop	Daph	Ostr
EB.r1	0d																								
	8d																								
	16d																								
	32d			4(A)								4		4											X
EB.r2	0d																								
	8d																								
	16d																								
	32d											4													X
EB.r3	0d																								
	8d														1								X		
	16d	1																							
	32d														4	4									X
FL.r1	0d																								
	8d																								
	16d																								
	32d															1		1	4						X
FL.r2	0d																								
	8d																								
	16d		1													1									
	32d															1		1							
FL.r3	0d																								
	8d																								
	16d																								
	32d																								

(continuation)

Code	Days	EphProc	EphCaen	ColNebr	ColLimn	ColOuli	ColEsol	ColAgab	ColDryo	DipErio	DipChi	DipCera	DipTab	DipSci	DipStr	DipOrth	OdoGom	Nem	Oli	ProHyd	PulPhy	HirErp	Cop	Daph	Ostr
F0. r1	0d																								
	8d														1										
	16d																								
	32d																		1	1					
F0. r2	0d																								
	8d																								
	16d																								
	32d																		2			1			
F0. r3	0d																								
	8d																								
	16d																								
	32d						1(L)						1						1	3		5			
LL. r1	0d																								
	8d																				1				X
	16d																							X	X
	32d							1(A)								1			1						
LL. r2	0d																								
	8d																								X
	16d																								X
	32d																		2						X
LL. r3	0d																								
	8d																								
	16d																								X
	32d										1														

(continuation)

Code	Days	EphProc	EphCaen	ColNebr	ColLimn	ColOuli	ColEsol	ColAgab	ColDryo	DipErio	DipChi	DipCera	DipTab	DipSci	DipStr	DipOrth	OdoGom	Nem	Oli	ProHyd	PulPhy	HirErp	Cop	Daph	Ostr
TE. r1	0d																								
	8d														1										X
	16d																								
	32d					4(A)													3						X
TE. r2	0d																								
	8d								1(L)																X
	16d																								
	32d				1(L)				2(L)									1	1						X
TE. r3	0d																								
	8d																								X
	16d																								
	32d														1										X
TO. r1	0d																								
	8d																								
	16d																1								
	32d											4				4			4						X
TO. r2	0d																								
	8d	2																	1						
	16d																								
	32d									4									2						X
TO. r3	0d																								
	8d	1																							
	16d	3																							
	32d		1																						X

Table S2.3. Selected traits and their respective categories. Traits are categorized based on their class, either resistance or resilience, which determines their adaptability during dry phases (rationale). Rationale is based in references indicated by numbers. The database column indicates the trait's source.

Trait	Category	Code	Resitance/ Resilience to face dry-phase	Rationale	DB
Resistance form	Yes (eggs, stoblasts, gemmules, cocoons, cells, diapause or dormancy)	RF.YES	**Resistance**	For inclusion in the seedbank[1,3]	8
	None	RF.NON			
Respiration	Aerial respiration (plastron, spiracle)	AER.RESP	**Resistance**	Favoured in wet habitats with low oxygen levels due to drying (e.g., isolated pools, HZ)[2,3]	8
	Aquatic respiration (tegument, gill)	AQ.RESP			
Locomotion	Capacity to move to HZ (Burrower, epibenthic; Interstitial, endobenthic)	SED.LOC	**Resistance**	Favouring migration to HZ[2]	8
	Other locomotion (Flier, swimmer, crawler, attached)	OTH.LOC			
Feeding Habits	Generalist (including taxa with both herbivore and detritivore habits)	FH.GEN	**Resistance**	Promoting habitation within the HZ[4]	8
	Non-generalist	FH.NOG			
Maximum body size	← 10 mm	SM.SIZE	**Resistance**	Favouring migration to HZ[2]	8
	→ 10 mm	LA.SIZE	**Resilience**	Associated with long dispersal distances and high fecundity[5]	
Life cycle duration	↖ 1 year	NCREQ1	**Resilience**	Enabling a short life cycle to evade desiccation during dry phase[2]	8
	→1 year	NCRM01			
Dispersal	Aquatic passive	AQUPAS			8
	Aquatic active	AQUACT			
	Aerial passive	AERPAS			
	Aerial active	AERACT	**Resilience**	For active dispersal to escape drying; and aerial adult stages[3,6]	

(continuation)

Trait	Category	Code	Resitance/ Resilience to face dry-phase	Rationale	DB
Female wing length (mm)	without	FWL0			9
	←5	FWL1			
	5 to 10	FWL2			
	10 to 15	FWL3			
	15 to 20	FWL4	**Resilience**	Related to larger body size, high fecundity; and better dispersers[5,6]	
	→20	FWL5	**Resilience**		
Potential number of reproduction cycles per year	←1	SEMIVO			8
	1	UNIVO			
	→1	PLURIVO	**Resilience**	Enabling to evade desiccation during dry phase[2]	
Adult stage	Aquatic adult stage (aquatic imago)	AAD.ST			8
	Terrestrial adult stage (non-aquatic imago)	TAD.ST	**Resilience**	Enabling to evade desiccation during dry phase[3]	

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Table S2.4. Total taxa abundances by assemblage type and stream. Abbreviations, assemblage type: Benthic, benthic; HZ, hyporheic; Seed, seedbank. Streams: EB, Ebre; FL, Fluvià; FO, Foix; LL, Llobregat; TE, Ter; TO, Tordera.

Group	Family	Genus	Code	Benthic assemblages						HZ				Invertebrate seedbank					
				EB	LL	FO	TO	FL	TE	EB	FO	TE	TO	EB	FL.	FO	LL	TE	TO
Bivalvia			Biv						15										
Coleoptera	Dryopidae	*Dryops*	ColDryo	1									1					3	
Coleoptera	Dytiscidae	*Agabus*	ColAgab	2													1		
Coleoptera	Dytiscidae	*Nebrioporus*	ColNebr											4					
Coleoptera	Dytiscidae		ColDyt		101			55	46										
Coleoptera	Elmidae	*Elmis*	ColElmi			5													
Coleoptera	Elmidae	*Esolus*	ColEsol										2			1			
Coleoptera	Elmidae	*Limnius*	ColLimn			5	425	78	108			1	1					1	
Coleoptera	Elmidae	*Oulimnius*	ColOuli	34		37				2	1							4	
Coleoptera	Hydraenidae	*Hydraena*	ColHydr				3												
Coleoptera	Hydrophilidae	*Hydrobius*	ColHydb		24			12	15										
Coleoptera	Scirtidae		ColSci			78													
Crustacea	Asellidae		CruAse	1		4	4	172	15										
Crustacea	Cambaridae	*Procambarus*	CruProc	3		25													
Crustacea	Gammaridae		CruGam			62				9	1								
Diptera	Athericidae		DipAth					1											
Diptera	Ceratopogonidae	Ceratopogoninae (subfamily)	DipCera	18			1638	7	177	6	3	3	16	8					4
Diptera	Ceratopogonidae	Forcipomyinae (subfamily)	DipForc									1							
Diptera	Ceratopogonidae		DipCer		541														
Diptera	Chironomidae	Orthocladiinae (subfamily)	DipOrth	1193						108	5	32	63	4	3		1		4
Diptera	Chironomidae	Tanypodinae (subfamily)	DipTanp	6						6			9						
Diptera	Chironomidae	Tanytarsini (Tribe)	DipTany	89						1			1						
Diptera	Chironomidae		DipChi		1035	1865	1224	783	864								1		
Diptera	Dixidae		DipDix			64													

(continuation)

Group	Family	Genus	Code	Benthic assemblages						HZ				Invertebrate seedbank					
				EB	LL	FO	TO	FL	TE	EB	FO	TE	TO	EB	FL.	FO	LL	TE	TO
Diptera	Dolichopodidae		DipDol	5															
Diptera	Empididae		DipEmp		58	46			35										
Diptera	Limoniidae	Eriopterini (Tribe)	DipErio																4
Diptera	Limoniidae		DipLim	1	11	376		38	4										
Diptera	Psychodidae		DipPsy		5			1	4										
Diptera	Sciomyzidae		DipSci											4					
Diptera	Simuliidae		DipSim	2	140	1700	64	3											
Diptera	Stratiomyidae		DipStr	1	3			39	54					5		1		2	
Diptera	Tabanidae		DipTab	2												1			
Diptera	Tipulidae		DipTip		41	20	65	98											
Diptera			Dip						15			5							
Ephemeroptera	Baetidae	*Baetis*	EphBaet			225	80				6								
Ephemeroptera	Baetidae	*Centroptilum*	EphCent		43			33	590										
Ephemeroptera	Baetidae	*Procloeon*	EphProc	20										1					6
Ephemeroptera	Caenidae	*Caenis*	EphCaen	193	63	119		13	157	7	3		4		1				1
Ephemeroptera	Ephemeridae	*Ephemera*	EphEphe						4										
Ephemeroptera	Heptageniidae	*Ecdyonurus*	EphEcdy								10								
Ephemeroptera	Leptophlebiidae	*Habroleptoides*	EphHabl				34	173	35										
Ephemeroptera	Leptophlebiidae		EphLep							1									
Hemiptera	Corixidae	*Micronecta*	HemMicr	4															
Hemiptera	Gerridae	*Gerris*	HemGerr			5													
Hirudinea	Erpobdellidae		HirErp													6			

(continuation)

Group	Family	Genus	Code	Benthic assemblages						HZ				Invertebrate seedbank					
				EB	LL	FO	TO	FL	TE	EB	FO	TE	TO	EB	FL.	FO	LL	TE	TO
Megaloptera	Sialidae	*Sialis*	MegSial						4										
Mollusca	Hydrobiidae		ProHyd		58						2					4			
Mollusca	Lymnaeidae		PulLym	1363	1363	73	68	127	625										
Mollusca	Physidae	*Physa*	PulPhys		41												1		
Mollusca	Physidae		PulPhy			5			4										
Mollusca	Planorbidae	*Ancylus*	PulAncy	4	261	5	151	212											
Nematomorpha			Nem	18	43	189	240			1	1	1	1		2			1	
Odonata	Aeshnidae	*Boyeria*	OdoBoye					1	23										
Odonata	Corduliidae		OdoCor		101		34	18											
Odonata	Gomphidae	*Gomphus*	OdoGomp	2															
Odonata	Gomphidae	*Onychogomphus*	OdoOnyc	8															
Odonata	Gomphidae		OdoGom							1									1
Odonata			Odo								1								
Oligochaeta			Oli	248	989	92	998	300	435	18	56	7	12		4	4	3	4	7
Plecoptera	Capniidae	*Capnia*	PleCapn	10			6			2									
Plecoptera	Leuctridae	*Leuctra*	PleLeuc					37											
Plecoptera	Nemouridae	*Nemoura*	PleNemo	13	66		34		62										
Trichoptera	Glossosomatidae		TriGlo								1								
Trichoptera	Hydropsychidae	*Hydropsyche*	TriHydr			64					1								
Trichoptera	Lepidostomatidae	*Crunoecia*	TriCrun					15											
Trichoptera	Lepidostomatidae	*Lepidostoma*	TriLepi					44											
Trichoptera	Limnephilidae		TriLim				4												
Trichoptera	Polycentropodidae		TriPol							2									

(continuation)

Group	Family	Genus	Code	Benthic assemblages						HZ				Invertebrate seedbank					
				EB	LL	FO	TO	FL	TE	EB	FO	TE	TO	EB	FL.	FO	LL	TE	TO
Trichoptera	Psychomyiidae	*Tinodes*	TriTino	1															
Trichoptera	Sericostomatidae	*Sericostoma*	TriSeri		54														

Table S2.5. Percentage breakdown of benthic taxa in hyporheic and seedbank assemblages. Abbreviations used are consistent with those in Table S2.4.

%	LL	FO	TO	FL	EB	TE
Seedbank	9.09	4.55	5.56	8.70	16	13.04
HZ	-	27.27	16.67	-	40	8.70

Table S2.6. Exclusive taxa enumerated by assemblage type. Benthic assemblages feature 33 exclusive taxa, whereas hyporheic and seedbank assemblages both contain 4 exclusive taxa each.

Assemblage type	Taxon	Number of individuals	Number of streams
Benthic	Bivalvia	15	1
Benthic	Coleoptera:*Elmis* sp	5	1
Benthic	Coleoptera:*Hydraena* sp	3	1
Benthic	Coleoptera:*Hydrobius* sp	51	3
Benthic	Coleoptera:Scirtidae fam.	78	1
Benthic	Crustacea:Asellidae fam.	196	5
Benthic	Crustacea:*Procambarus* sp	28	2
Benthic	Diptera:Athericidae fam.	1	1
Benthic	Diptera:Dixidae fam.	64	1
Benthic	Diptera:Dolichopodidae fam.	5	1
Benthic	Diptera:Empididae fam.	139	3
Benthic	Diptera:Psychodidae fam.	10	3
Benthic	Diptera:Simuliidae fam.	1909	5
Benthic	Diptera:Tipulidae fam.	224	4
Benthic	Ephemeroptera:*Centroptilum* sp	666	3
Benthic	Ephemeroptera:*Ephemera* sp	4	1
Benthic	Ephemeroptera:*Habroleptoides* sp	242	3
Benthic	Hemiptera:*Micronecta* sp	4	1
Benthic	Hemiptera:*Gerris* sp	5	1
Benthic	Megaloptera:*Sialis* sp	4	1
Benthic	Odonata:*Boyeria* sp	24	2
Benthic	Odonata:Corduliidae fam	153	3
Benthic	Odonata:*Gomphus* sp	2	1
Benthic	Odonata:*Onycogomphus* sp	8	1
Benthic	Plecoptera:*Leuctra* sp	37	1
Benthic	Plecoptera:*Nemoura* sp	175	4
Benthic	Mollusca:Lymnaeidae fam.	3619	6
Benthic	Mollusca:*Ancylus* sp	633	5
Benthic	Trichoptera:*Crunoecia* sp	15	1

TABLE S2.6
(continuation)

Assemblage type	Taxon	Number of individuals	Number of streams
Benthic	Trichoptera:*Lepidostoma* sp	44	1
Benthic	Trichoptera: Limnephilidae fam.	4	1
Benthic	Trichoptera:*Tinodes* sp	1	1
Benthic	Trichoptera:*Sericostoma* sp	54	1
HZ	Diptera:Foripomyiinae subfam.	1	1
HZ	Ephemeroptera:*Ecdyonurus* sp	10	1
HZ	Trichoptera:Glossosomatidae fam.	1	1
HZ	Trichoptera:Polycentropodidae fam.	2	1
Seedbank	Coleoptera:*Nebrioporus* sp	4	1
Seedbank	Diptera:*Eriopterini* sp	4	1
Seedbank	Diptera:Sciomyzidae fam.	4	1
Seedbank	Hirudinea:Erpobdellidae fam.	6	1

Table S2.7. Index values calculated for each sample. Assemblage types are abbreviated are stated in Table S2.4. Abbreviations: H', diversity index; S, taxon richness; FRic, functional richness; FDis, functional dispersion.

Stream	Assemblage type	H'	S	FRic	FDis
EB	Benthic	1.31	24	0.73	0.21
EB	HZ	1.34	13	0.25	0.22
EB	Seed	1.67	6	0.07	0.35
FL	Benthic	1.83	22	0.60	0.35
FL	Seed	1.28	4	←0.01	0.31
FO	Benthic	1.85	22	0.43	0.25
FO	HZ	1.58	13	0.20	0.32
FO	Seed	1.62	6	0.14	0.32
LL	Benthic	2.12	21	0.56	0.31
LL	Seed	1.48	5	0.04	0.31
TE	Benthic	2.17	23	0.64	0.33
TE	HZ	1.49	8	0.06	0.29
TE	Seed	1.66	6	0.05	0.32
TO	Benthic	1.89	17	0.40	0.30
TO	HZ	1.59	11	0.15	0.26
TO	Seed	1.78	7	0.19	0.36

Table S2.8. Spearman correlations between axes and specific trait categories. The abbreviations for traits are detailed in Table S2.3.

Trait Categories	A1	A2	A3	A4	A5
RF.YES	0.39	0.03	-0.43	0.46	-0.23
RF.NON	-0.39	-0.03	0.43	-0.46	0.23
SED.LOC	0.29	0.07	-0.04	0.02	-0.16
OTH.LOC	-0.29	-0.07	0.04	-0.02	0.16
NCREQ1	-0.47	**0.64**	-0.13	0.47	0.03
NCRMO1	0.47	**-0.64**	0.13	-0.47	-0.03
FH.NOG	**0.83**	-0.22	0.22	0.33	0.26
FH.GEN	**-0.83**	0.22	-0.22	-0.33	-0.26
fwl1	-0.36	**-0.62**	-0.33	0.32	0.18
fwl2	-0.16	**0.61**	0.49	-0.03	-0.19
fwl3	0.08	0.41	0.3	-0.2	-0.33
fwl4	0.34	0.19	0.09	-0.03	-0.36
fwl5	**0.53**	-0.01	0	-0.21	-0.01
SEMIVO	**0.59**	-0.08	-0.27	-0.34	0.05
UNIVO	-0.18	0	0.39	-0.02	-0.25
PLURIVO	-0.37	0.16	-0.24	0.41	-0.03
AQUPAS	-0.1	-0.3	**-0.50**	-0.08	0.17
AERPAS	-0.07	0.22	-0.28	0.47	-0.04
AQUACT	-0.03	0.22	0.27	-0.01	-0.28
AERACT	0.17	0.09	**0.59**	-0.25	0.07
SM.SIZE	**-0.74**	-0.01	0.21	0.05	**0.53**
LA.SIZE	**0.74**	0.01	-0.21	-0.05	**-0.53**
AER.RESP	-0.12	-0.31	**0.65**	0.34	-0.18
AQU.RESP	0.12	0.31	**-0.65**	-0.34	0.18
TAD.ST	0.08	**0.83**	0.01	0.07	0.21
AAD.ST	-0.08	**-0.83**	-0.01	-0.07	-0.21

Table S2.9. Abundance-weighted trait categories by assemblage.

Stream	Assemblage type	Trait Category	Abundance-weighted trait	Trait class
EB	Benthic	RF.YES	0.21	Resistance
FL	Benthic	RF.YES	0.51	Resistance
FO	Benthic	RF.YES	0.68	Resistance
LL	Benthic	RF.YES	0.68	Resistance
TE	Benthic	RF.YES	0.55	Resistance

TABLE S2.9
(continue)

Stream	Assemblage type	Trait Category	Abundance-weighted trait	Trait class
TO	Benthic	RF.YES	0.48	Resistance
EB	Seedbank	RF.YES	0.42	Resistance
FL	Seedbank	RF.YES	0.52	Resistance
FO	Seedbank	RF.YES	0.72	Resistance
LL	Seedbank	RF.YES	0.48	Resistance
TE	Seedbank	RF.YES	0.39	Resistance
TO	Seedbank	RF.YES	0.28	Resistance
EB	HZ	RF.YES	0.15	Resistance
FL	HZ	RF.YES	0	Resistance
FO	HZ	RF.YES	0.39	Resistance
LL	HZ	RF.YES	0	Resistance
TE	HZ	RF.YES	0.2	Resistance
TO	HZ	RF.YES	0.14	Resistance
EB	Benthic	SED.LOC	0.34	Resistance
FL	Benthic	SED.LOC	0.33	Resistance
FO	Benthic	SED.LOC	0.28	Resistance
LL	Benthic	SED.LOC	0.23	Resistance
TE	Benthic	SED.LOC	0.23	Resistance
TO	Benthic	SED.LOC	0.27	Resistance
EB	Seedbank	SED.LOC	0.2	Resistance
FL	Seedbank	SED.LOC	0.29	Resistance
FO	Seedbank	SED.LOC	0.3	Resistance
LL	Seedbank	SED.LOC	0.27	Resistance
TE	Seedbank	SED.LOC	0.23	Resistance
TO	Seedbank	SED.LOC	0.37	Resistance
EB	HZ	SED.LOC	0.34	Resistance
FL	HZ	SED.LOC	0	Resistance
FO	HZ	SED.LOC	0.18	Resistance
LL	HZ	SED.LOC	0	Resistance
TE	HZ	SED.LOC	0.29	Resistance
TO	HZ	SED.LOC	0.32	Resistance
EB	Benthic	FH.GEN	0.88	Resistance
FL	Benthic	FH.GEN	0.74	Resistance
FO	Benthic	FH.GEN	0.88	Resistance
LL	Benthic	FH.GEN	0.9	Resistance
TE	Benthic	FH.GEN	0.6	Resistance
TO	Benthic	FH.GEN	0.92	Resistance
EB	Seedbank	FH.GEN	0.69	Resistance
FL	Seedbank	FH.GEN	0.7	Resistance

(continue)

Stream	Assemblage type	Trait Category	Abundance-weighted trait	Trait class
FO	Seedbank	FH.GEN	0.6	Resistance
LL	Seedbank	FH.GEN	0.86	Resistance
TE	Seedbank	FH.GEN	0.93	Resistance
TO	Seedbank	FH.GEN	0.93	Resistance
EB	HZ	FH.GEN	0.84	Resistance
FL	HZ	FH.GEN	0	Resistance
FO	HZ	FH.GEN	0.58	Resistance
LL	HZ	FH.GEN	0	Resistance
TE	HZ	FH.GEN	0.83	Resistance
TO	HZ	FH.GEN	0.79	Resistance
EB	Benthic	SM.SIZE	0.76	Resistance
FL	Benthic	SM.SIZE	0.39	Resistance
FO	Benthic	SM.SIZE	0.69	Resistance
LL	Benthic	SM.SIZE	0.38	Resistance
TE	Benthic	SM.SIZE	0.69	Resistance
TO	Benthic	SM.SIZE	0.55	Resistance
EB	Seedbank	SM.SIZE	0.46	Resistance
FL	Seedbank	SM.SIZE	0.48	Resistance
FO	Seedbank	SM.SIZE	0.31	Resistance
LL	Seedbank	SM.SIZE	0.47	Resistance
TE	Seedbank	SM.SIZE	0.67	Resistance
TO	Seedbank	SM.SIZE	0.65	Resistance
EB	HZ	SM.SIZE	0.68	Resistance
FL	HZ	SM.SIZE	0	Resistance
FO	HZ	SM.SIZE	0.24	Resistance
LL	HZ	SM.SIZE	0	Resistance
TE	HZ	SM.SIZE	0.56	Resistance
TO	HZ	SM.SIZE	0.6	Resistance
EB	Benthic	AER.RESP	0.07	Resistance
FL	Benthic	AER.RESP	0.21	Resistance
FO	Benthic	AER.RESP	0.23	Resistance
LL	Benthic	AER.RESP	0.13	Resistance
TE	Benthic	AER.RESP	0.08	Resistance
TO	Benthic	AER.RESP	0.15	Resistance
EB	Seedbank	AER.RESP	0.42	Resistance

TABLE S2.9
(continue)

Stream	Assemblage type	Trait Category	Abundance-weighted trait	Trait class
FL	Seedbank	AER.RESP	0.24	Resistance
FO	Seedbank	AER.RESP	0.29	Resistance
LL	Seedbank	AER.RESP	0.28	Resistance
TE	Seedbank	AER.RESP	0.54	Resistance
TO	Seedbank	AER.RESP	0.25	Resistance
EB	HZ	AER.RESP	0.05	Resistance
FL	HZ	AER.RESP	0	Resistance
FO	HZ	AER.RESP	0.16	Resistance
LL	HZ	AER.RESP	0	Resistance
TE	HZ	AER.RESP	0.12	Resistance
TO	HZ	AER.RESP	0.06	Resistance
EB	Benthic	NCREQ1	0.88	Resilience
FL	Benthic	NCREQ1	0.59	Resilience
FO	Benthic	NCREQ1	0.77	Resilience
LL	Benthic	NCREQ1	0.63	Resilience
TE	Benthic	NCREQ1	0.78	Resilience
TO	Benthic	NCREQ1	0.69	Resilience
EB	Seedbank	NCREQ1	0.78	Resilience
FL	Seedbank	NCREQ1	0.67	Resilience
FO	Seedbank	NCREQ1	0.42	Resilience
LL	Seedbank	NCREQ1	0.49	Resilience
TE	Seedbank	NCREQ1	0.35	Resilience
TO	Seedbank	NCREQ1	0.78	Resilience
EB	HZ	NCREQ1	0.85	Resilience
FL	HZ	NCREQ1	0	Resilience
FO	HZ	NCREQ1	0.32	Resilience
LL	HZ	NCREQ1	0	Resilience
TE	HZ	NCREQ1	0.75	Resilience
TO	HZ	NCREQ1	0.81	Resilience
EB	Benthic	FWL5	0.01	Resilience
FL	Benthic	FWL5	0.01	Resilience
FO	Benthic	FWL5	0.01	Resilience
LL	Benthic	FWL5	0.02	Resilience
TE	Benthic	FWL5	0	Resilience
TO	Benthic	FWL5	0.01	Resilience
EB	Seedbank	FWL5	0	Resilience
FL	Seedbank	FWL5	0	Resilience
FO	Seedbank	FWL5	0	Resilience
LL	Seedbank	FWL5	0	Resilience

(continue)

Stream	Assemblage type	Trait Category	Abundance-weighted trait	Trait class
TE	Seedbank	FWL5	0	Resilience
TO	Seedbank	FWL5	0.04	Resilience
EB	HZ	FWL5	0.01	Resilience
FL	HZ	FWL5	0	Resilience
FO	HZ	FWL5	0.01	Resilience
LL	HZ	FWL5	0	Resilience
TE	HZ	FWL5	0	Resilience
TO	HZ	FWL5	0	Resilience
EB	Benthic	PLURIVO	0.65	Resilience
FL	Benthic	PLURIVO	0.32	Resilience
FO	Benthic	PLURIVO	0.53	Resilience
LL	Benthic	PLURIVO	0.41	Resilience
TE	Benthic	PLURIVO	0.55	Resilience
TO	Benthic	PLURIVO	0.39	Resilience
EB	Seedbank	PLURIVO	0.53	Resilience
FL	Seedbank	PLURIVO	0.55	Resilience
FO	Seedbank	PLURIVO	0.17	Resilience
LL	Seedbank	PLURIVO	0.4	Resilience
TE	Seedbank	PLURIVO	0.14	Resilience
TO	Seedbank	PLURIVO	0.52	Resilience
EB	HZ	PLURIVO	0.6	Resilience
FL	HZ	PLURIVO	0	Resilience
FO	HZ	PLURIVO	0.24	Resilience
LL	HZ	PLURIVO	0	Resilience
TE	HZ	PLURIVO	0.54	Resilience
TO	HZ	PLURIVO	0.52	Resilience
EB	Benthic	AERACT	0.18	Resilience
FL	Benthic	AERACT	0.11	Resilience
FO	Benthic	AERACT	0.16	Resilience
LL	Benthic	AERACT	0.14	Resilience
TE	Benthic	AERACT	0.18	Resilience
TO	Benthic	AERACT	0.27	Resilience
EB	Seedbank	AERACT	0.37	Resilience
FL	Seedbank	AERACT	0.08	Resilience
FO	Seedbank	AERACT	0.2	Resilience
LL	Seedbank	AERACT	0.14	Resilience

TABLE S2.9
(continue)

Stream	Assemblage type	Trait Category	Abundance-weighted trait	Trait class
TE	Seedbank	AERACT	0.35	Resilience
TO	Seedbank	AERACT	0.25	Resilience
EB	HZ	AERACT	0.18	Resilience
FL	HZ	AERACT	0	Resilience
FO	HZ	AERACT	0.07	Resilience
LL	HZ	AERACT	0	Resilience
TE	HZ	AERACT	0.17	Resilience
TO	HZ	AERACT	0.19	Resilience
EB	Benthic	LA.SIZE	0.24	Resilience
FL	Benthic	LA.SIZE	0.61	Resilience
FO	Benthic	LA.SIZE	0.31	Resilience
LL	Benthic	LA.SIZE	0.62	Resilience
TE	Benthic	LA.SIZE	0.31	Resilience
TO	Benthic	LA.SIZE	0.45	Resilience
EB	Seedbank	LA.SIZE	0.54	Resilience
FL	Seedbank	LA.SIZE	0.52	Resilience
FO	Seedbank	LA.SIZE	0.69	Resilience
LL	Seedbank	LA.SIZE	0.53	Resilience
TE	Seedbank	LA.SIZE	0.33	Resilience
TO	Seedbank	LA.SIZE	0.35	Resilience
EB	HZ	LA.SIZE	0.27	Resilience
FL	HZ	LA.SIZE	0	Resilience
FO	HZ	LA.SIZE	0.38	Resilience
LL	HZ	LA.SIZE	0	Resilience
TE	HZ	LA.SIZE	0.32	Resilience
TO	HZ	LA.SIZE	0.3	Resilience
EB	Benthic	TAD.ST	0.84	Resilience
FL	Benthic	TAD.ST	0.44	Resilience
FO	Benthic	TAD.ST	0.89	Resilience
LL	Benthic	TAD.ST	0.43	Resilience
TE	Benthic	TAD.ST	0.7	Resilience
TO	Benthic	TAD.ST	0.62	Resilience
EB	Seedbank	TAD.ST	0.85	Resilience
FL	Seedbank	TAD.ST	0.4	Resilience
FO	Seedbank	TAD.ST	0.15	Resilience
LL	Seedbank	TAD.ST	0.29	Resilience
TE	Seedbank	TAD.ST	0.13	Resilience
TO	Seedbank	TAD.ST	0.74	Resilience
EB	HZ	TAD.ST	0.82	Resilience

Stream	Assemblage type	Trait Category	Abundance-weighted trait	Trait class
FL	HZ	TAD.ST	0	Resilience
FO	HZ	TAD.ST	0.2	Resilience
LL	HZ	TAD.ST	0	Resilience
TE	HZ	TAD.ST	0.61	Resilience
TO	HZ	TAD.ST	0.76	Resilience

Table S3.1. Characterization of the study sites. Hydrological measurements were collected for a total period of 370 days. AC: Algars after the confluence. Values (Mean ± SE) are the mean of the four field campaigns. Site E11 was always dry when we went to the field.

Site	Latitude, N	Longitude, E	Altitude m.a.s.l.	Strahler Order	Sub-basin	Subcatch. Area (ha)	N-NO_2 (µg N/L)	N-NO_3 (µg N/L)	N-NH_4 (µg N/L)	Temperature (ºC)
E10	40° 51' 54"	0° 19' 3"	568	2	L'Estrets	2902.4	2.3 ± 0.8	986.3 ± 421.4	11.3 ± 1.9	13.7 ± 0.8
E11	40° 52' 4"	0° 19' 5"	574	2	L'Estrets	485.3	NA	NA	NA	NA
E12	40° 52' 0"	0° 18' 27"	555	1	L'Estrets	217.0	1.0 ± 0	201.8 ± 14.9	16.0 ± 4.6	13.1 ± 1.2
E13	40° 52' 32"	0° 18' 22"	540	1	L'Estrets	2902.4	1.0 ± 0	218.7 ± 47.4	12.0 ± 4.4	10.4 ± 0.8
E14	40° 53' 9"	0° 18' 2"	510	3	L'Estrets	2902.4	1.0 ± 0	236.0 ± 72.5	10.7 ± 3.4	12.8 ± 2.2
E15	40° 53' 55"	0° 17' 11"	474	2	L'Estrets	590.4	5.0 ± NA	89.0 ± NA	15.0 ± NA	8.3 ± 1.1
E16	40° 56' 8"	0° 16' 32"	417	3	L'Estrets	2902.4	3.8 ± 1.7	4259.3 ± 1945.8	24.0 ± 7.4	15.8 ± 1.8
A1	40° 50' 56"	0° 15' 21"	559	2	L'Algars	4233.2	1.0 ± 0	159.5 ± 51.1	17.0 ± 3.5	13.4 ± 1.5
A2	40° 52' 13"	0° 15' 18"	518	2	L'Algars	4233.2	1.0 ± 0	91.8 ± 26.7	12.5 ± 2.8	14 ± 2.3
A3	40° 53' 11"	0° 14' 42"	487	3	L'Algars	4233.2	5.0 ± 3.4	550.5 ± 357.0	14.3 ± 1.6	14.3 ± 2.1
A4	40° 56' 20"	0° 16' 26"	413	4	L'Algars AC	2993.7	11.5 ± 6.3	5226.8 ±1285.8	23.3 ± 1.4	13.6 ± 1.9
A5	40° 58' 23"	0° 17' 29"	382	4	L'Algars AC	9684.8	8.8 ± 2.3	3741.8 ± 1463.4	19.8 ± 4.2	12.1 ± 3.1
A6	41° 2' 3"	0° 15' 7"	311	4	L'Algars AC	9684.8	8.0 ± 2.6	3850.3 ± 1380.3	22.7 ± 4.7	14.2 ± 2.7
A7	41° 2' 35"	0° 14' 1"	293	4	L'Algars AC	10924.1	8.0 ± 2.5	2773.7 ± 1417.9	28.3 ± 7.8	12.8 ± 1.9
A8	41° 6' 22"	0° 12' 33"	217	4	L'Algars AC	10924.1	4.7 ± 0.9	1995.7 ± 1221.8	31.0 ± 19.2	14.9 ± 3.1
A9	41° 12' 20"	0° 15' 4"	136	4	L'Algars AC	8207.9	9.3 ± 1.9	3612.7 ± 954.3	23.3 ± 9.3	15.3 ± 3.1

Table S3.2. Pairwise Pearson correlations of annual predictor variables. Values in bold correspond to highly correlated variables.

	Flow intermittence		Chemical water characteristics					Canopy	Catchment land-uses		
	Non-flow periods	Non-flow days	Ca	Mg	DIN	DOC	Conductivity		Urban	Agricultural	Natural
Non-flow periods	1	0.33	0.12	0.13	-0.10	0.11	0.35	0.39	0.24	0.20	-0.20
Non-flow days	0.33	1	0.33	0.56	-0.29	-0.03	0.27	0.36	0.05	-0.31	0.31
Ca	0.12	0.33	1	**0.90**	0.32	0.67	**0.84**	-0.44	0.66	0.36	-0.36
Mg	0.13	0.56	**0.90**	1	0.23	0.36	0.64	-0.40	0.63	0.27	-0.27
DIN	-0.10	-0.29	0.32	0.23	1	0.24	0.28	-0.59	0.22	**0.83**	**-0.83**
DOC	0.11	-0.03	0.67	0.36	0.24	1	**0.80**	-0.27	0.29	0.29	-0.29
Conductivity	0.35	0.27	**0.84**	0.64	0.28	**0.80**	1	-0.36	0.65	0.33	-0.33
Canopy	0.39	0.36	-0.44	-0.40	-0.59	-0.27	-0.36	1	-0.39	-0.42	0.42
Urban	0.24	0.05	0.66	0.63	0.22	0.29	0.65	-0.39	1	0.36	-0.36
Agricultural	0.20	-0.31	0.36	0.27	**0.83**	0.29	0.33	-0.42	0.36	1	**-1.00**
Natural	-0.20	0.31	-0.36	-0.27	**-0.83**	-0.29	-0.33	0.42	-0.36	**-1.00**	1

Table S3.3. Total taxa abundances by assemblage type and stream. Abbreviations, assemblage type: Benthic, benthic; HZ, hyporheic; Seed, seedbank. Streams: EB, Ebre; FL, Fluvià; FO, Foix; LL, Llobregat; TE, Ter; TO, Tordera.

Reach	Days	Mg (mg Mg/L)	Ca (mg Ca/L)	DOC (mg C/L)	DIN (µg N/L)	Non-flow days	Non-flow periods	Conductivity (µS/cm)	Temperature (ºC)
E10	365	4.57	30.49	22.08	999.75	148	4	318.00	13.33
E10	90	8.87	39.99	14.97	1471.00	14	1	327.05	12.40
E11	365	NA	NA	NA	NA	370	0	NA	NA
E12	365	6.96	43.36	54.01	218.75	0	0	537.73	12.83
E12	90	13.37	54.83	40.02	197.50	0	0	533.95	11.15
E13	365	7.92	40.83	56.22	231.67	108	1	489.27	10.37
E13	90	11.61	45.62	41.38	278.50	0	0	488.60	9.70
E14	365	6.18	34.54	41.72	247.67	105	2	437.60	12.20
E14	90	9.02	38.74	33.21	296.50	0	0	438.35	9.45
E15	365	12.24	43.91	2.91	109.00	316	1	297.15	8.30
E15	90	12.24	43.91	2.91	109.00	84	1	297.15	8.30
E16	365	5.05	29.98	32.61	4287.00	19	1	430.75	15.43
E16	90	9.32	31.41	25.74	4431.00	0	0	427.65	11.60
A1	365	5.78	35.90	29.98	177.50	0	0	372.50	14.50
A1	90	11.16	45.69	22.28	241.50	0	0	375.25	10.50
A2	365	4.77	31.15	25.55	105.25	0	0	338.23	13.35
A2	90	9.16	40.43	19.93	141.00	0	0	345.90	9.45
A3	365	6.63	37.35	34.36	569.75	55	1	412.28	15.05
A3	90	12.64	47.95	25.64	258.50	0	0	369.80	10.20
A4	365	7.16	38.91	34.93	5261.50	0	0	443.53	13.93
A4	90	13.51	49.18	24.66	3924.00	0	0	401.10	9.90
A5	365	7.50	45.27	40.77	3770.25	0	0	442.47	13.98

(continuation)

Reach	Days	Mg (mg Mg/L)	Ca (mg Ca/L)	DOC (mg C/L)	DIN (µg N/L)	Non-flow days	Non-flow periods	Conductivity (µS/cm)	Temperature (°C)
A5	90	13.51	55.88	24.73	4865.00	0	0	417.30	9.20
A6	365	9.90	46.50	33.91	3881.00	20	1	421.43	15.25
A6	90	13.97	52.78	25.84	4567.00	20	1	359.15	10.20
A7	365	10.40	48.60	32.22	2810.00	0	0	456.13	12.07
A7	90	14.72	54.27	24.83	3777.5	0	0	422.20	9.80
A8	365	11.82	55.66	44.66	2031.33	179	3	986.13	12.30
A8	90	16.60	57.96	31.77	2939.50	0	0	454.75	10.10
A9	365	13.46	68.73	100.97	3645.33	169	2	1086.85	12.67
A9	90	18.16	67.45	51.87	3242.50	21	1	582.70	10.60

Table S3.4. Principal components: explained variance.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Standard deviation	1.974	1.532	1.091	0.965	0.552	0.384	0.331	0.246	0.103
Proportion of Variance	0.433	0.261	0.132	0.104	0.034	0.016	0.012	0.007	0.001
Cumulative Proportion	0.433	0.694	0.826	0.930	0.964	0.980	0.992	0.999	1

Table S3.5. Principal components: weights or loadings.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Agricultural land-uses	0.303	-0.265	0.578	-0.081	0.288	0.368	0.458	-0.258	0.047
Non-flow periods	0.088	0.466	0.550	0.159	-0.432	0.216	-0.099	0.450	-0.039
Non-flow days	0.111	0.563	0.069	-0.392	-0.027	-0.512	0.371	-0.227	0.243
Ca	0.470	0.115	-0.218	-0.058	0.271	0.242	-0.294	0.213	0.672
Mg	0.407	0.194	-0.210	-0.450	0.217	0.163	-0.060	0.195	-0.659
DIN	0.288	-0.400	0.415	-0.156	0.016	-0.589	-0.449	0.102	-0.035
DOC	0.366	0.019	-0.145	0.654	0.208	-0.342	0.390	0.294	-0.133
Canopy cover	-0.292	0.401	0.261	0.241	0.679	-0.035	-0.348	-0.179	-0.115
Conductivity	0.446	0.154	-0.076	0.315	-0.324	0.070	-0.278	-0.683	-0.136

Table S3.6. Means and standard error (se) of decomposition rates.

Site	K_d	se (K_d)	K_{dd}	se (K_{dd})
A1	3.02E-04	7.24E-05	2.55E-05	6.60E-06
A2	5.59E-04	3.70E-05	6.26E-05	4.26E-06
A3	9.59E-04	1.11E-04	9.83E-05	1.13E-05
A4	2.41E-03	2.10E-04	2.47E-04	2.22E-05
A5	4.37E-03	4.40E-04	4.16E-04	3.15E-05
A6	9.77E-04	6.12E-05	9.33E-05	4.15E-06
A7	7.09E-04	9.65E-05	6.60E-05	9.93E-06
A8	1.83E-04	9.19E-05	1.68E-05	8.81E-06
A9	9.90E-04	1.33E-04	8.11E-05	1.04E-05
E10	1.42E-03	3.37E-04	1.13E-04	2.69E-05
E11	1.02E-04	8.38E-05	9.24E-06	7.74E-06
E12	7.35E-04	1.48E-04	6.94E-05	1.39E-05
E13	2.79E-04	1.26E-04	2.58E-05	1.21E-05
E14	2.62E-04	4.83E-05	1.93E-05	3.88E-06
E15	1.28E-04	2.89E-05	1.83E-05	4.34E-06
E16	6.49E-04	1.61E-04	5.42E-05	1.35E-05

Table S3.7. Summary of multiple linear regression model selected for K_{dd}: $\log(K_{dd}) \sim \sqrt{DIN} + \sqrt{Non-flow\ days} + \sqrt{canopy}$. *NFD*: non-flow days; *canopy*: canopy cover (%); *DIN*: total dissolved inorganic nitrogen (µg/L). P – value ← 0.001 '***', ← 0.01 '**', ←0.05 '*', ←0.1 '.'.

Residuals:

Min	1Q	Median	3Q	Max
-0.86907	-0.37609	0.01434	0.17814	1.31490

Coefficients:

	Estimate	Std. Error	t value	Pr(→|t|)
(Intercept)	-9.7143	0.1587	-61.207	2.74e-15 ***
DIN	0.8426	0.2327	3.621	0.00402 **
NFD	-0.4658	0.1715	-2.716	0.02008 *
canopy	0.5407	0.2375	2.277	0.04378 *

Residual standard error: 0.6147 on 11 degrees of freedom

Multiple R^2: 0.6672 **Adjusted R^2**: 0.5764

F-statistic: 7.35 on 3 and 11 DF **p-value:** 0.005633**

Table S3.8. Means and standard errors (se) of ergosterol and fungal biomass at each site and extraction time (days).

Site	Days	Ergosterol (µg g^{-1})	se (ergosterol)	Fungal biomass (µg g^{-1})	se (fungal biomass)
A1	90	13.21	5.35	2.40	0.97
A2	90	20.00	7.29	3.64	1.33
A3	90	16.12	5.12	2.93	0.93
A4	90	165.62	24.30	30.11	4.42
A5	90	186.71	19.35	33.95	3.52
A6	90	12.26	0.74	2.23	0.14
A7	90	41.92	9.37	7.62	1.70
A8	90	6.92	2.24	1.26	0.41
A9	90	18.82	6.30	3.42	1.15
E10	90	171.04	15.45	31.10	2.81
E11	90	7.56	1.72	1.37	0.31
E12	90	9.30	4.31	1.69	0.78
E13	90	33.76	14.67	6.14	2.67
E14	90	7.69	1.08	1.40	0.20
E15	90	2.83	0.37	0.51	0.07
E16	90	25.02	7.02	4.55	1.28
A1	365	47.57	21.29	8.65	3.87
A2	365	90.48	16.48	16.45	3.00
A4	365	240.83	95.4	43.79	17.35
A5	365	149.61	52.83	27.20	9.61
A8	365	8.98	2.57	1.63	0.47
A9	365	151.91	14.35	27.62	2.61
E10	365	157.57	43.71	28.65	7.95
E11	365	10.88	4.27	1.98	0.78
E12	365	92.36	13.39	16.79	2.43
E13	365	55.55	14.63	10.10	2.66
E15	365	34.70	2.30	6.31	0.42
E16	365	113.54	22.05	20.64	4.01

Table S3.9. Summary of linear regression model between k_{dd} and fungal biomass: $\log(k_{dd}) \sim \log(fungal\ biomass) : Time$. Decomposition rates ($k_{dd}$) is expressed on degree days^{-1}. Fungal biomass (bioM) is the mean at each point and at each time and it is expressed as mg of fungal biomass per g of dry mass. Time is a factor with two levels (90 days and 365 days).

Residuals:

Min	1Q	Median	3Q	Max
-0.9609	-0.4850	-0.1275	0.5246	1.4813

Coefficients:

	Estimate	Std. Error	t value	Pr(→|t|)
(Intercept)	-11.008	0.239	-45.978	← 2e-16 ***
Log(bioM):90days	0.774	0.139	5.560	8.82e-05 ***
Log(bioM):365days	0.528	0.112	4.709	7.92e-05 ***

Residual standard error: 0.7034 on 25 degrees of freedom

Multiple R^2: 0.5852 **Adjusted R^2:** 0.5521

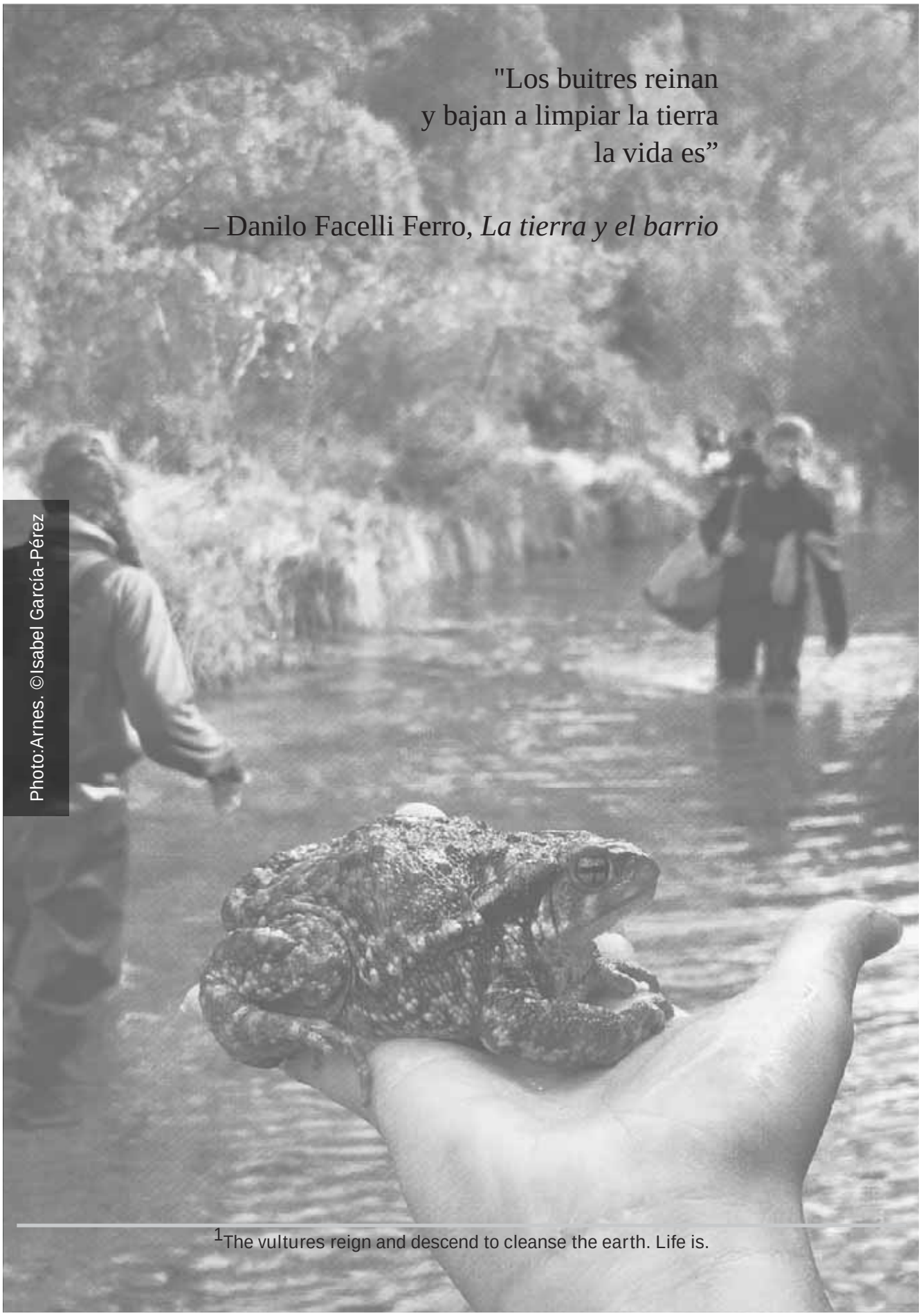
F-statistic: 17.64 on 2 and 25 DF **p-value:** 1.669e-05

Table S3.10. Summary of mixed model selected for fungal biomass: $\log(fungal\ biomass) \sim \sqrt{DIN} + \sqrt{Non-flow\ days} + \sqrt{canopy} + Days + (1|Point)$. *NFD*: non-flow days; *canopy*: canopy cover (%); *DIN*: total dissolved inorganic nitrogen (µg/L); *Days [365]*: the fixed effects estimate the differences of Days[365] to Days[90]. *Estimates*: estimated coefficients; *CI*: confidence interval; σ^2: variance of residual; $\tau_{00\ Point}$: variance of random effect (Point); *ICC*: variance explained by random effect. *Marginal* R^2: the variance of the fixed effects; *Conditional* R^2: the variance of both the fixed and random effects.

Fixed Effects	logbioM		
Predictors	*Estimates*	*CI*	*p-value*
(Intercept)	1.13	0.66 – 1.59	**<0.001**
NFD	-0.36	-0.74 – 0.03	0.069
canopy	0.77	0.26 – 1.27	**0.003**
DIN	1.03	0.55 – 1.51	**<0.001**
Days [365]	1.64	0.95 – 2.33	**<0.001**
Random Effects			
σ^2	0.56		
$\tau_{00\ Point}$	0.17		
ICC	0.23		
N_{Point}	15		
Observations	26		
Marginal R^2 / Conditional R^2	0.607 / 0.699		

ORIGINAL PUBLICATIONS





"Los buitres reinan
y bajan a limpiar la tierra
la vida es"

– Danilo Facelli Ferro, *La tierra y el barrio*

Photo:Arnes. ©Isabel García-Pérez

[1]The vultures reign and descend to cleanse the earth. Life is.

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Aquatic Sciences

RESEARCH ARTICLE

The role of seedbanks and hyporheic refuges in supporting benthic invertebrate community resistance and resilience to dry phases

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Abstract
In intermittent streams, aquatic organisms use various strategies to face dry phases, but the relative contribution of these strategies to persist during dry phase remains unclear. Here, we investigated the in situ persistence of benthic invertebrates in the saturated hyporheic sediments and the "invertebrate seedbank" that persists in dry sediments across six Mediterranean intermittent streams. Taxonomic and functional responses within hyporheic and seedbank assemblages were compared with those in the benthic assemblages under connected flow conditions by combining field and mesocosms data. The dry phase duration in each stream was calculated to assess the responses of hyporheic and seedbank assemblages. Taxonomic composition and abundance-weighted traits related to resistance and resilience to face the dry phase in each assemblage type (benthic, hyporheic, seedbank) were determined. Taxonomic (richness and diversity) and functional (richness and dispersion) metrics were also calculated. We found that seedbank and hyporheic assemblages supported up to 16% and 40% of the benthic taxa, respectively. Only taxonomic and functional richness differed between assemblage types. Contrary to previous research, no clear relationship was established between diversity or the abundance of resistance traits and the duration of dry phase; however, a negative linear relationship was identified between the abundance of resilience traits and the duration of the dry phase. The increase in the frequency and duration of drying events due to climate change will reduce water availability in both saturated and unsaturated streambed sediments, compromising the persistence of aquatic biodiversity in intermittent streams.

Keywords Species trait · Macroinvertebrate · IRES · Functional diversity · Dry period · Flow intermittence

Introduction

Intermittent streams, characterized by shifts between wet and dry in-stream conditions, comprise more than 50% of global river networks (Messager et al. 2021). Flow interruption in these streams occurs gradually and varies in both time and space, modifying the lateral, longitudinal, and vertical dimensions of hydrological connectivity during different hydrological phases (Datry et al. 2014). Flow contraction can culminate in the complete loss of surface water during the dry phase. The dry phase affects ecosystem functions, such as organic matter processing and sediment transport, as well as riparian and aquatic biodiversity (Larned et al. 2010). Aquatic invertebrate communities in intermittent streams have various adaptations to face dry phases, including the use of remaining wet habitats as refuges, as hyporheic zone (HZ), or the capacity to persist within dry sediment, as a "seedbank" (Stubbington and Datry 2013). However, the contribution of both hyporheic refuge and invertebrate seedbank, as used by benthic

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communities to persist during dry phases, have not yet been compared (Hay et al. 2018; DelVecchia et al. 2022). In the context of global change, in which the spatial and temporal distribution of many intermittent streams is predicted to increase (Döll and Schmied 2012; Sauquet et al. 2021), understanding how invertebrates persist in situ during dry phases in wet and dry sediments, i.e., in the hyporheic zone and invertebrate seedbank, is necessary to inform actions that preserve their biodiversity (Datry et al. 2018).

Drying alters community composition, with reductions in taxonomic and functional diversity increasing with dry-phase severity (Arias-Real et al. 2021; Crabot et al. 2021b). In natural intermittent streams, communities are adapted to drying, displaying different combinations of functional traits that promote resistance and/or resilience to face dry phases (Nimmo et al. 2015; Bogan et al. 2015). Resilience strategies enable communities to recover after flow resumption by aquatic or aerial dispersal from refuges including upstream, downstream, and/or nearby perennial reaches. Active dispersal can also enable escape of dry conditions to wet refuges, following environmental cues as flow recedes, potentially supporting subsequent community recovery (Drummond et al. 2015). In contrast, resistance strategies enable organisms to persist in situ during dry phases (Bogan et al. 2017). For instance, during dry phases, some invertebrates can use isolated pools in streambeds (Bonada et al. 2006) or move to the subsurface sediments of the HZ (Stubbington 2012; DelVecchia et al. 2022).

The capacity of the HZ to act as a refuge for aquatic invertebrates during dry phases varies spatially and temporally, influenced by factors such as sediment composition, moisture content, and water quality (Stubbington 2012). Should the dry phase persist, water levels within the HZ may also decline, affecting taxonomic composition and leading to the loss of desiccation-sensitive taxa (Stubbington et al. 2009). After the water table recedes through the subsurface, aquatic invertebrates can only persist in damp streambed sediments as invertebrate seedbanks, which include desiccation-tolerant life stages, such as dormant eggs or juveniles (Tronstad et al. 2005). Partially desiccation-tolerant taxa can also survive within the invertebrate seedbank, provided some sediment moisture remains (Loskotová et al. 2021). The invertebrate seedbank can support over 50% of benthic taxa, and it can make a particularly substantial contribution to community recovery in certain areas, such as isolated catchments or reaches without saturated HZ (Stubbington and Datry 2013). However, some taxa are eliminated as their taxon-specific desiccation-tolerance thresholds are surpassed (Stubbington et al. 2016). Hyporheic refuge and the invertebrate seedbank are well-documented individually, but how benthic invertebrates use these different in situ strategies to face dry phases remains unclear.

Our aim was to characterize the relative contributions of the hyporheic refuge and the invertebrate seedbank to supporting the persistence of benthic aquatic invertebrates in situ during dry phases in intermittent streams, by combining field data with mesocosm experiments. We predicted that (1) the taxonomic and functional diversity of hyporheic and seedbank assemblages will represent subsets of benthic communities, resulting in lower taxonomic and functional diversity; (2) the dry phase will result in a higher abundance of traits that confer resistance to these conditions in invertebrates from seedbank and the HZ, compared with those in benthic communities. This is because benthic taxa present in hyporheic refuge and invertebrate seedbank possess traits enabling them to tolerate dry phases. Specifically, the capacity to move into the HZ will be more abundant in taxa from HZ, whereas the ability to persist by using any desiccation-tolerant life stage will be more abundant among taxa from invertebrate seedbank; and (3) streams experiencing prolonged dry phases will show reduced taxonomic and functional diversity in hyporheic and seedbank assemblages, and an increased abundance of resistance traits, attributed to the decline in desiccation-sensitive taxa.

Methods

Study sites

We sampled six reaches, one in each of six intermittent Mediterranean streams across Catalonia on the northeastern Iberian Peninsula (Fig. 1), during the summer of 2020. Selected sites had similar geology, stream order, and stream width. Specifically, stream orders spanned from three to four across an altitudinal range of 110–526 m a.s.l. The geology of streams was characterized by sandstone, granite, and marl formations, with the streambeds primarily composed of gravel and coarse sand. All streams had a natural flow intermittence, experiencing dry-phase durations between 16 and 69 days, starting between early and late summer. Throughout the study period, only two reaches (Tordera and Ebro) did not dry completely as they retained pools in the streambed (personal observation). Flow resumed almost simultaneously across all streams with the onset of autumn rains in mid-September 2020, following our dry phase sample collection (Table S1).

Field methods

Hydrological characterization

In June 2020, before the dry phase started, a temperature data logger (HOBO Pendant MX2201, Onset Corp, Bourne, MA, USA) was installed in the middle of each streambed,

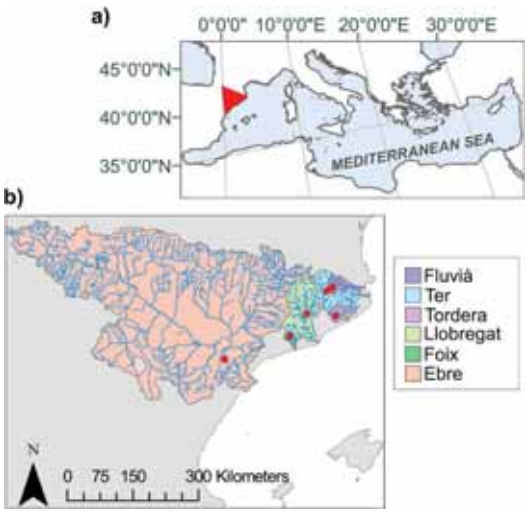


Fig. 1 **a** Location of the study area in Catalonia (NE Iberian Peninsula); **b** location of the six intermittent streams, indicated by red points

avoiding deep pools to obtain a more representative record of the flow disconnection in the stream. Hourly temperatures were recorded until the moment of sampling collection in early September 2020. We calculated the number of days without surface water (the dry-phase duration) for each stream using the daily temperature variation between the maximum and minimum streambed temperatures. This variation indicates water presence due to the higher specific heat capacity of water compared with air (Smith 1975). As a result, daily variability in temperatures is lower when water is present. Air temperature and rainfall data from proximate meteorological stations were utilized to elucidate any anomalies in daily temperature fluctuations, by comparing direct measurements of air temperature and precipitation patterns with the presence of flow. However, the presence of surface water can vary within a stream reach because drying occurs more quickly in riffles than in pools (Hwan and Carlson 2016).

Sample collection

To characterize invertebrate seedbanks, we excavated sediment samples from three points in each streambed at the end of the summer, just before the onset of autumn rainfalls, using a hand trowel. These points were selected for their lower slope, which favors the deposition of sediments. Larger surface clasts (> 5 cm) were intentionally avoided, and the depth of collection was restricted to a maximum of 15 cm. Each sampled area ranged from 0.5 to 2 m^2. Approximately 8 L of dry sediment were collected at every reach, with an attempt to collect the same quantity from each area (~2.5–3 L). The sediments collected from each area were combined and transported to the laboratory.

We collected three replicate hyporheic water samples from a depth of 40 cm at 15–20 m intervals along the dry reach. Because hyporheic exchange flow can vary between riffles and pools (Käser et al. 2009), we exclusively sampled in riffle zones to minimize differences. To maximize richness estimates using a Bou–Rouch pump (Bou and Rouch 1967), we tried to pump 20 L of hyporheic water for each replicate. However, on several occasions, we were unable to find hyporheic water and had to reposition the pump multiple times to locate it where feasible. Consequently, we were able to extract a total of 60 L of hyporheic water from only one reach, while from three other reaches, we extracted between 35 and 50 L. The HZ in two reaches, Llobregat and Fluvià, was not sampled because they were dry at the sampled depth (Table S1). The pumped water was filtered through a 250 µm mesh to retain invertebrates (Sánchez-Morales et al. 2018).

Benthic invertebrates were collected at each reach just after the rainy season (February) to ensure that all streams were in the flowing phase and connected. We collected 5 min kick samples with a 250 µm net following a standardized multihabitat protocol that represented each habitat in proportion to its occurrence (Jáimez-Cuéllar et al. 2002).

Seedbank mesocosm setup

In the laboratory, we sieved 7.5 L of dry sediment from each reach through a 0.5 cm test sieve to remove large sediment grains. We then distributed it into three 8 L containers and covered each container with a 1 mm mesh to minimize external colonization and to retain emerging invertebrates. The containers were immediately flooded with 5 L of dechlorinated tap water, continuously aerated with air stones, and maintained at room temperature under a natural photoperiod of 13:11 h (light/dark). We sampled the water column using a 250 µm hand net for 30 s at 0, 8, 16, and 32 days to collect invertebrates. After 32 days, the experiment was stopped, and all invertebrates in the sediment were collected (Datry et al. 2012) by filtering the column water and screening the sediments from each mesocosm.

Invertebrate data

All invertebrates were identified to genus except for Diptera (which were identified to the subfamily or family level), Oligochaeta (identified to the subclass level), Nematoda (identified to the phylum level), and individuals that were too small for accurate identification. Micro-crustaceans were also observed, noting only their presence or absence at the class level (Ostracoda and Copepoda) and at the genus level

(Daphnia), without quantifying their abundance (Table S2). We aggregated all replicate samples to calculate global community diversity indices and for data analysis due to the low number of individuals per sample and the high incidence of zeros in the replicate hyporheic samples and invertebrate seedbank samples. Relative abundances, rather than absolute abundances, were calculated because different methods were used to sample each assemblage type (benthic, hyporheic, seedbank). As a result, we obtained six samples for each type of assemblage, except for hyporheic assemblages.

Resistance and resilience traits

To assess the functional aspects of each prediction, we selected and classified trait categories that promote resistance and resilience during dry phases, considering both as distinct trait classes. We considered traits associated with resistance, including any desiccation-tolerant life stages (resistance forms' trait), aerial respiration (spiracle or plastron), the capacity to move into the HZ, generalist feeding habits (herbivorous and detritivorous habits; Cummins 1973), and small body size, as resistance trait categories. We classified female wing size, large body size, aerial active dispersal, multivoltine capacity, short life cycle duration ($\leq$ 1 year), and terrestrial adult life stage as resilience trait categories (Table S3). Trait data were compiled from Múria et al. (2020) and Sarremejane et al. (2020). Values were assigned to represent the affinity of each taxon for each trait category, taking into account differences among taxa within the same genus (referred to as potential trait adaptability) using a fuzzy code approach (Chevenet et al. 1994). All category scores were standardized to proportions by setting the category sum to 1. Our final trait set had a total of 27 categories belonging to 11 traits.

For each assemblage, we calculated an abundance-weighted trait matrix by multiplying the taxa–trait matrix by the relative abundance taxa matrix (Statzner et al. 2004). Furthermore, we calculated the average abundance-weighted values for each trait class (resistance or resilience) across each assemblage type.

Taxonomic and functional metrics

To represent invertebrate seedbank "importance" (sensu Stubbington and Datry 2013), we calculated the percentage of benthic taxa present in the HZ and the invertebrate seedbank for each stream. We also identified taxa that occurred exclusively in each assemblage type. Additionally, we calculated taxonomic richness (S) and the Shannon–Wiener index (H') (Shannon 1948) for each assemblage.

To describe functional diversity, we built a functional space (FS) using the taxa–trait matrix that included all taxa from all assemblages (72 taxa) and all trait categories. The taxa–trait matrix was used to generate a dissimilarity matrix based on the Gower distances adapted to fuzzy coding traits (Pavoine et al. 2009). The FS was created using a principal coordinates analysis conducted with the dudi.pco function from the R package ade4 (Dray and Dufour 2007). We selected the five most informative axes based on their ability to represent the original trait-based dissimilarity among taxa (Maire et al. 2015). The 5-D FS explained 71.90% of the Gower dissimilarity matrix (with a mean squared deviation of 0.009). To identify the traits associated with each FS axis, we utilized Spearman correlation coefficients (Múria et al. 2020). In addition, the FS was used to obtain two functional diversity metrics. The first metric, functional richness (FRic), was calculated as the minimum hypervolume of the FS occupied by invertebrate taxa in each assemblage (Villéger et al. 2008). Low values of FRic suggest that taxa capable of responding to environmental disturbance may be absent (Mason et al. 2005). The second metric, functional dispersion (FDis), represented the weighted mean distance of all invertebrate taxa to the weighted centroid of their assemblage within the FS (Laliberté and Legendre 2010), being equivalent to the multivariate dispersion (Anderson et al. 2006). FRic and FDis are complementary metrics; FRic captures the range of the FS covered by each assemblage, whereas FDis focuses on the variation in their trait abundances (Kuebbing et al. 2018). Both metrics were calculated using the R package FD (Laliberté and Legendre 2010; Laliberté et al. 2014).

Data analysis

To test differences between assemblage types in all metrics (taxonomic and functional metrics and the mean of abundance-weighted traits by trait class), we used the non-parametric Kruskal−Wallis test (Ostertagová et al. 2014). Additionally, post hoc pairwise comparison tests were performed between assemblage types using a Wilcoxon rank sum test (Wilcoxon 1945) with a Bonferroni correction to a significance level at $p < 0.05$.

To assess the effect of dry-phase duration on the resilience and resistance of aquatic invertebrates in hyporheic and seedbank assemblages, we fitted linear and nonlinear regressions, utilizing nonlinear least squares for parameter estimation in the latter (Smyth 2002). We used only data from hyporheic and seedbank assemblages, with dry-phase duration as the explanatory variable, and the mean of abundance-weighted traits for each trait class, along with their different diversity metrics, as the different response variables. The effect of dry-phase duration on individual abundance-weighted trait categories was also tested using the same approach. For linear regressions (LM), residuals were visually examined for normality and homoscedasticity. All data were analyzed using R (R Core Team 2022).

Results

Taxonomic diversity

We identified a total of 24,487 individuals: belonging to 49 families and 41 genera, which included 23,970 from 34 taxa in the benthic assemblages, 415 from 24 taxa in the hyporheic assemblages, and 102 from 21 taxa in the invertebrate seedbank (Table S4). Four groups each accounted for more than 5% individuals of the benthic assemblages: Diptera (51.46%), Mollusca (18.19%), Oligochaeta (12.77%), and Ephemeroptera (7.43%). Three groups each accounted > 5% individuals of the hyporheic assemblages: Diptera (62.41%), Oligochaeta (22.41%), and Ephemeroptera (7.47%). Finally, five groups each accounted > 5% individuals of the seedbank assemblages: Diptera (41.18%), Oligochaeta (21.57%), Coleoptera (13.73%), Ephemeroptera (8.82%), and Hirudinea (5.88%). Diptera was the only order present in all seedbanks. Nematomorpha, Coleoptera, and Ephemeroptera were present in all hyporheic assemblages.

Seedbank and hyporheic invertebrates represented 4.5–16% and 8.7–40% of benthic taxa, respectively (Table S5). Four taxa were exclusively found in invertebrate seedbanks (*Nebrioporus* sp., Eriopterini, Sciomyzidae, Erpobdellidae), with each taxon limited to a single stream. Similarly, four taxa were exclusive to the HZ (*Ecdyonurus* sp., Forcipomyiinae, Glossosomatidae, Polycentropodidae), each restricted to a single stream. Thirty-three taxa were present only in benthic assemblages (e.g., *Micronecta* sp. and *Sericostoma* sp.), but only the family Lymnaeidae was encountered in all benthic assemblages (Table S6).

Taxonomic richness was highest for benthic assemblages ($S = 22 \pm 2$ taxa per sample), moderate for hyporheic assemblages (11 ± 2 taxa), and lowest for seedbank assemblages (6 ± 1 taxa) (Kruskal–Wallis: $\chi^2 = 13.353$; d.f. = 2, $p = 0.0013$; associated Wilcoxon paired test: 0.01 < all Bonferroni p-adjusted < 0.05; Fig. 2a). The Shannon−Wiener index was comparable in all assemblages, showing values between 1.50 ± 0.12 and 1.86 ± 0.31 (Kruskal–Wallis: $\chi^2 = 5.5772$; d.f. = 2, $p = 0.0615$; Fig. 2b).

Functional diversity

The first two axes of the FS jointly explained 43.77% of the original trait variation, with axes 1 and 2 explaining 23.79% and 19.98%, respectively (Fig. 3a). Axis 1 was highly correlated (> 0.50, Spearman correlation) with feeding habit, body size, voltinism, and female wing length, aligning with the resistance trait categories at one extreme (generalist

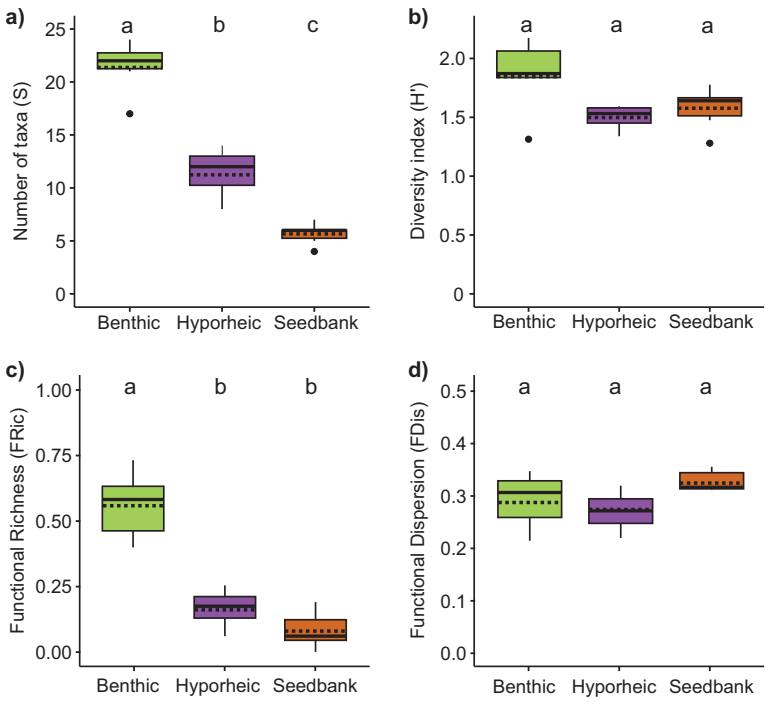


Fig. 2 Taxonomic (**a**, **b**) and functional (**c**, **d**) metric values for benthic, hyporheic and seedbank assemblages: **a** taxonomic richness (*S*), **b** Shannon−Wiener diversity (H'), **c** functional richness (FRic), and **d** functional dispersion (FDis). Solid lines represent the median, while dashed lines represent the mean. Different letters indicate statistically significant differences among assemblage types

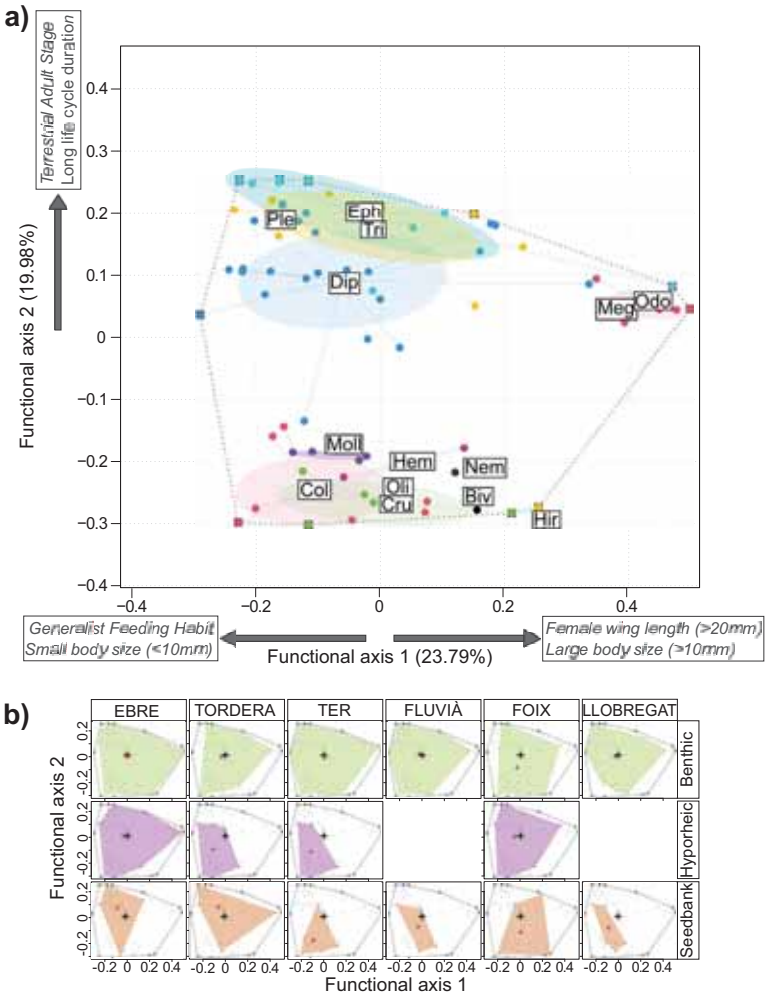


Fig. 3 Functional space (FS) plot on two axes: **a** FS with taxa represented by points colored according to taxonomic group. The dotted line denotes the boundary of the total FS created by all taxa. Categories of selected traits that are correlated with each axis are located at the corresponding axis extreme. **b** FS occupied by each assemblage, with small points representing individual taxa; red crosses indicating the assemblage centroids; and black crosses marking the centroid of the all-taxa ordination. *Biv* Bivalvia, *Col* Coleoptera, *Cru* Crustacea, *Dip* Diptera, *Eph* Ephemeroptera, *Hem* Hemiptera, *Hir* Hirudinea, *Meg* Megaloptera, *Moll* Mollusca, *Nem* Nematomorpha, *Oli* Oligochaeta, *Odo* Odonata, *Ple* Plecoptera, *Tri* Trichoptera

feeding habits and small body size) and the resilience trait categories at the other (large body size and high female wing length). Axis 2 was highly correlated (> 0.50, Spearman correlation) with adult life stage, life cycle duration, and female wing length, primarily corresponding to the resilience trait categories at one of its extremes (terrestrial adult stage and a life cycle duration of 1 year or less; Table S8). Orders plotted in three main clusters: Diptera, Ephemeroptera, Plecoptera, and Trichoptera in the upper left-hand quadrant; Odonata and Megaloptera with positive axis 1 values; and all eight other orders with negative axis 2 values (Fig. 3a).

Benthic assemblages occupied more functional space than their respective hyporheic and seedbank assemblages (Fig. 3b). Two hyporheic assemblages occupied > 50% of the total FS, while the other two hyporheic assemblages occupied less space. All seedbank assemblages occupied < 50% of the FS, and the two smallest FS corresponded to the streams without HZ (Fig. 3b). Functional richness was highest for benthic assemblages (0.58 ± 0.11), and lowest for hyporheic (0.06 ± 0.01) and seedbank (0.05 ± 0.01) assemblages (Kruskal–Wallis: $\chi^2 = 11.765$; d.f. = 2, $p = 0.0028$; associated Wilcoxon paired test: Bonferroni p-adjusted$_{\text{all benthic}} = 0.014$; Fig. 2c). Functional dispersion was not significantly different among assemblage types, showing values between 0.27 ± 0.05 and 0.32 ± 0.03 (Kruskal–Wallis: $\chi^2 = 4.0772$; d.f. = 2, $p = 0.1302$; Fig. 2d).

Resistance and resilience traits

The mean of abundance-weighted resistance trait categories was lowest for hyporheic assemblages (0.25 ± 0.20), and highest for benthic assemblages (0.47 ± 0.05) and seedbank assemblages (0.35 ± 0.11) (Kruskal–Wallis: $\chi^2 = 11.486$; d.f. = 2, $p = 0.0032$; associated Wilcoxon paired test: Bonferroni p-adjusted$_{\text{all hyporheic}} = 0.015$; Fig. 4a). Generalist feeding habits were the predominant resistance trait category across all assemblage types, with weighted abundances ranging from 0.51 ± 0.14 to 0.82 ± 0.13. This was closely followed by the small body size, with weighted abundances between 0.35 ± 0.31 and 0.58 ± 0.17. The capacity to move into the HZ demonstrated moderate weighted abundances in both benthic (0.28 ± 0.05) and hyporheic (0.19 ± 0.06) assemblages, whereas the abundance of a resistance forms' trait was more pronounced in dry sediment (0.47 ± 0.15) (Table S9). Two trait categories varied among the assemblage types: resistance forms' trait, which was lowest for HZ (Kruskal–Wallis: $\chi^2 = 9.7996$; d.f. = 2, $p = 0.0074$; associated Wilcoxon paired test: 0.02 < Bonferroni p-adjusted$_{\text{hyporheic}} < 0.04$), and aerial respiration, which was highest for the seedbank (Kruskal–Wallis: $\chi^2 = 13.066$; d.f. = 2, $p = 0.0015$; associated Wilcoxon paired test: 0.006 < Bonferroni p-adjusted$_{\text{all seedbank}} < 0.02$).

The mean of abundance-weighted resilience trait categories was statistically comparable in all assemblages, showing values between 0.25 ± 0.21 and 0.41 ± 0.04 (Kruskal–Wallis: $\chi^2 = 1.8382$; d.f. = 2, $p = 0.3989$; Fig. 4a). A short life cycle duration (≤ 1 year) was the predominant resilience trait category for all assemblage types, with weighted abundances ranging from 0.45 ± 0.40.01 to 0.72 ± 0.11. In benthic and hyporheic assemblages, this was followed by the terrestrial adult stage (0.65 ± 0.20 and 0.40 ± 0.38, respectively) and multivoltinism (0.47 ± 0.13 and 0.32 ± 0.28, respectively). In contrast, in seedbank assemblages, large body size and terrestrial adult stage were the subsequent most abundant trait categories (0.50 ± 0.14 and 0.42 ± 0.30, respectively).

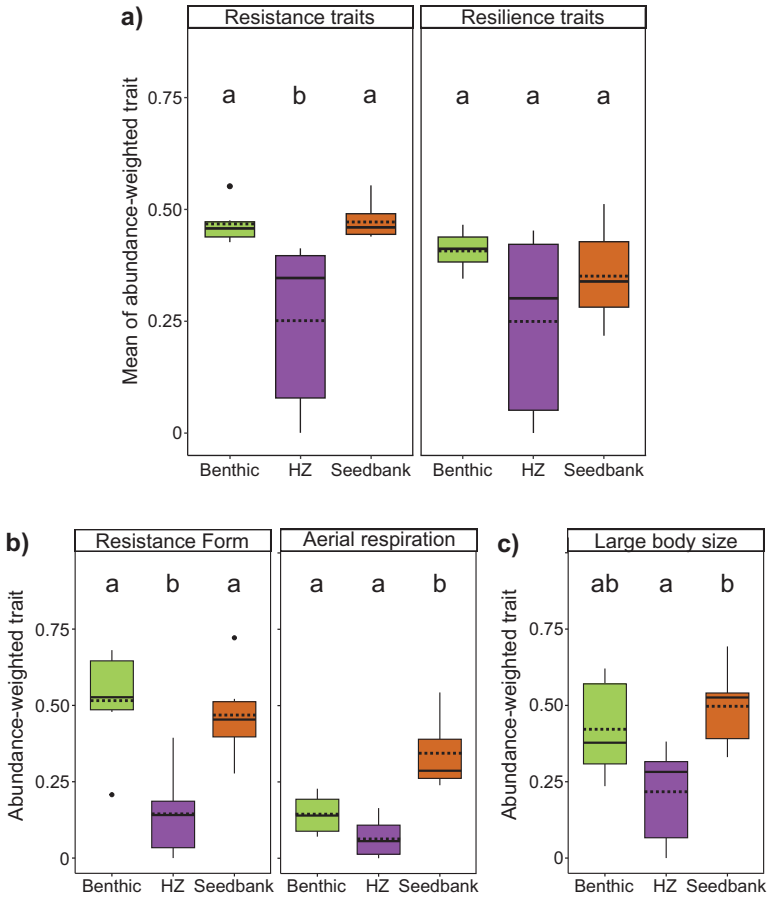


Fig. 4 Abundance-weighted traits for benthic, hyporheic, and seedbank assemblages: **a** mean of abundance-weighted trait by trait class; **b** resistance categories, and **c** resilience category. Solid lines indicate the median, and dashed lines represent the mean. Traits and trait categories are described in Table S2. Different letters indicate statistically significant differences

Notably, large body size varied among the assemblage types (Kruskal–Wallis: $\chi^2 = 6.8843$; d.f. = 2, $p = 0.032$; associated Wilcoxon paired test: Bonferroni p-adjusted$_{\text{seedbank–hyporheic}} = 0.039$; Fig. 4c).

Effects of dry-phase duration on taxonomic and functional assemblages

Only the mean of abundance-weighted resilience traits differed in response to dry-phase duration in hyporheic and seedbank assemblages following a linear regression (LM: $F_{1,8} = 17.75$; d.f. = 8, $p = 0.0029$). Notably, as the dry-phase duration increased, the abundance of these traits decreased (Fig. 5a). Specifically, both the terrestrial adult stage (LM: $F_{1,8} = 34.9$; d.f. = 8, $p = 0.0003$) and short life cycle duration (LM: $F_{1,8} = 14.51$; d.f. = 8, $p = 0.0052$) also followed a negative linear relationship with the dry-phase duration (Fig. 5b). However, taxonomic and functional metrics, along with the mean of abundance-weighted resistance traits, did not conform to any discernible model (Fig. S1).

Discussion

This study is the first to compare the contribution of seedbank and hyporheic refuge used by benthic aquatic invertebrates to face dry phases in situ in intermittent streams. Our results showed that persistence in the seedbank and the HZ are strategies employed by a subset of benthic invertebrate taxa during dry phases in Mediterranean streams. Taxonomic and functional richness were higher in benthic assemblages than in those in the HZ and in invertebrate seedbanks, confirming our initial hypothesis that both hyporheic and seedbank assemblages are subsets of benthic assemblages. Contrary to our second hypothesis, no significant differences in the abundance-weighted resistance traits were observed between benthic and seedbank assemblages; consistently, hyporheic assemblages showed the lowest abundances. Finally, while no clear relationship was established between diversity or the abundance of resistance traits, and the duration of dry phases, as was expected, a linear negative relationship was identified between the abundance of resilience traits and the duration of the dry phase.

Contribution of hyporheic and seedbank invertebrate assemblages supporting benthic communities

Consistent with our first hypothesis, nearly all taxa and traits observed in the HZ and invertebrate seedbanks were also identified in benthic communities, which showed the highest taxonomic and functional richness. These findings suggest that hyporheic and seedbank assemblages represent subsets of the benthic communities (Stubbington 2012; Stubbington and Datry 2013). The taxonomic overlap among all assemblage types, ranging between 5% and 40%, demonstrated that some benthic taxa might persist in the HZ and/or the seedbank. Concretely, the percentage of benthic taxa in the HZ (8.7–40%) corresponded to some previous studies. For instance, Boulton (1992) found that 35% and 69% of

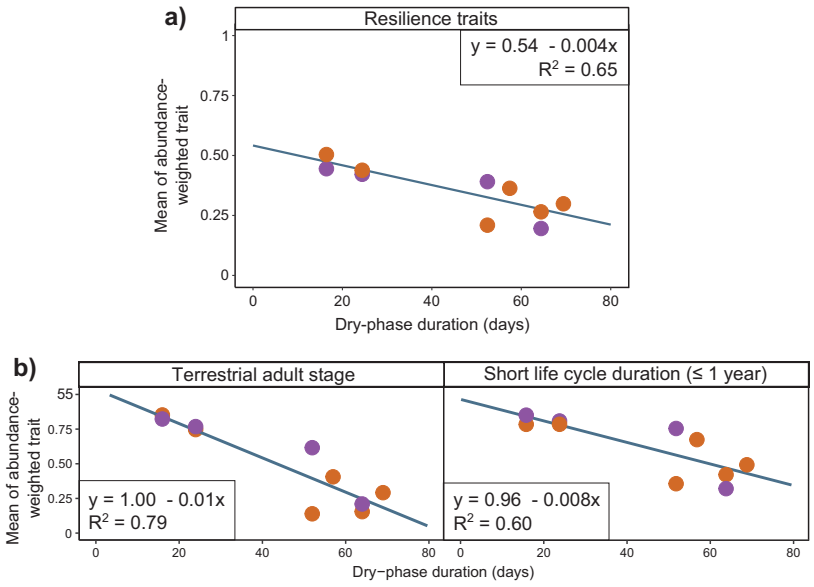


Fig. 5 Linear relationship between dry-phase duration and (**a**) the mean of abundance-weighted resilience traits and (**b**) the terrestrial adult stage and short life cycle duration, both categories of resilience traits. Lilac points represent hyporheic assemblages, whereas orange points represent seedbank assemblages. Benthic assemblages were excluded

benthic taxa were present in the HZ of temperate and arid intermittent streams, respectively. However, the taxonomic richness in these sites was limited to 8 and 10 taxa, similar to the taxonomic richness found in the HZ of our study (between 8 and 13 taxa). In contrast, Datry (2012) reported a 75% overlap of benthic taxa in HZ in a temperate stream but noted a 10% decrease in similarity between benthic and hyporheic assemblages for every 10 days of prolonged dry-phase duration. On the other hand, the percentage of benthic taxa found in the invertebrate seedbanks in our study streams (between 4.5% and 16%) was lower than in previous studies. For example, Datry et al. (2012) found two to three times more benthic taxa in the invertebrate seedbank of a temperate intermittent stream under similar dry-phase durations. However, these percentages varied from 33% to 5%, in arid and Mediterranean streams, respectively, with low taxonomic richness (9 and 3, respectively), similar to our findings (Stanley et al. 1994; Chester and Robson 2011).

Oligochaeta and Diptera were abundant in the studies previously mentioned (Boulton 1992; Chester and Robson 2011; Datry 2012; Datry et al. 2012). In our streams, both Oligochaeta and multiple Diptera families were also well represented in all assemblage types. Both groups include taxa with desiccation-tolerant life stages and the capacity to move into the HZ, with certain Oligochaeta species also having aerial respiration (Tachet et al. 2010). Moreover, these groups include semi-aquatic species, explaining their potential to be among the few taxa that persist in invertebrate seedbanks during extended dry phases (Tronstad et al. 2005; Chester and Robson 2011; Datry et al. 2012; Stubbington et al. 2016). Some Ephemeroptera found in the HZ, such as *Caenis* sp., are characterized as a burrower and can actively move into the HZ (Tachet et al. 2010; Robertson 2010). However, the early instars of *Ecdyonurus* sp. and *Baetis* sp. are transported passively into the HZ by down-welling water, resulting in their temporary inhabitation of these subsurface sediments (Boulton 2000; Tachet et al. 2010). On the other hand, Ephemeroptera found in seedbanks, including *Procloeon* sp. and *Caenis* sp., have summer egg diapause (Clifford 1982; Brittain 1990). Coleoptera taxa identified in the HZ can move into this refuge, whereas none of those recorded in the seedbank (e.g., *Nebrioporus* sp.) are recognized as having desiccation-tolerant life stages (Tachet et al. 2010). The survival of these Coleoptera in the dry streambed can be attributed to their aerial respiration and certain level of desiccation tolerance, conferred by their impermeable protective cuticle (Holdgate 1956; Pallarés et al. 2017).

We identified seven benthic taxa in the HZ that were not present in the invertebrate seedbanks, such as *Hydropsyche* sp., which does not show desiccation-tolerant life stages (Tachet et al. 2010). Conversely, six benthic taxa were found in the invertebrate seedbanks but not in the HZ, such as *Procloeon* sp., which enters summer diapause and is multivoltine, adaptations for avoiding aquatic environments during the dry phase (Bonada et al. 2007a, b). Furthermore, four taxa exclusively in the HZ, with three represented by one to two individuals, and *Ecdyonurus* sp. by ten individuals in a single sample. Conversely, four taxa were only found in the invertebrate seedbank, each represented by four to six individuals per sample. Given the very low densities of these taxa in both the HZ and in invertebrate seedbanks, we suggest that they may also have been present in the benthic sediments but were missed by kick sampling. This method captures only a proportion of the taxa present (e.g., 62% and 78% of families and 50% and 68% of species in 3 and 6 min sampling, respectively; Furse et al. 1981).

Differences in trait responses across assemblage types

Contrary to our second prediction, the hyporheic assemblages showed the lowest abundance-weighted resistance traits, in part because small body size, generalist feeding habits, and the capacity to move into the HZ were common resistance traits in benthic and seedbank, as well as hyporheic assemblages. These traits are either directly or indirectly associated with the ability to move into and persist within the HZ. For instance, body size affects an organism's ability to penetrate sediment due to the dimensions of interstitial pathways (Stubbington 2012), while generalist feeding habits are advantageous given the limited abundance and diversity of food resources in the HZ (Burrell and Ledger 2003). In addition, a few hyporheic taxa (e.g., Glossosotomidae and Forcipomyinae), although not burrowers, show crawler behavior and small sizes, enabling them to seek refuge in the HZ following the water table receding through the subsurface sediments in dry phases (Vander Vorste et al. 2016; Maazouzi et al. 2017). This ability is influenced by interactions between taxon characteristics (i.e., their traits) and environmental factors, including sediment characteristics, such as grain size, and local hydrological conditions, such as the direction and strength of hyporheic exchange (Stubbington 2012; Dole-Olivier et al. 2022).

Seedbank and benthic assemblages had similar abundances of resistance traits, with the third most abundant trait in seedbank assemblages being the presence of resistance forms. In contrast, aerial respiration showed low-weighted abundances (<0.4) across all assemblages, and had its highest abundance in seedbank assemblages. Although aerial respiration becomes particularly advantageous when water flow decreases and water quality deteriorates, especially when dissolved oxygen concentrations decline (Bonada et al. 2007b; Mellado-Díaz et al. 2007), it is not necessarily associated with the persistence in HZ or in invertebrate seedbanks, even though if some taxa have both trait classes. For instance, within the Mollusca, most freshwater pulmonates

can tolerate hypoxic conditions, as may occur in the HZ during dry phases, and also tolerate exposure to air. They can also extend this tolerance by entering a dormant, aestivating state (Poznańska et al. 2015).

On the other hand, we did not find differences in abundance-weighted resilience traits between assemblage types. The only exception was the large body size trait category, which showed the lowest abundances in hyporheic assemblages, suggesting that maximum body size may limit the use of HZ (Mathers et al. 2019). The similar trait composition across assemblage types and the taxonomic and functional overlapping (see above), reflect the dominance of traits that enable aquatic invertebrates to tolerate dry phases in intermittent natural streams of Mediterranean basin (Bonada et al. 2007a).

Dry-phase duration and resistance strategies

Contrary to our third hypothesis, taxonomic and functional diversity, as well as resistance traits, did not show a clear relationship with the duration of dry phase in hyporheic refuges and seedbanks. Despite the limited number of samples and total individuals, we identified a negative correlation between abundance-weighted resilience traits and the duration of dry phase. As dry-phase duration increases, environmental conditions become harsher, filtering out the less desiccation-tolerant taxa (Datry 2012; Datry et al. 2012), which may also possess resilience traits. In addition, we found that the resilience trait categories of terrestrial adult stage and short life cycle duration (≤ 1 year) also showed a negative linear relationship with dry phase duration. The decline of these traits may indicate avoidance behavior in response to harsher conditions during more severe dry phases (Strachan and Chester 2015). However, we must be cautious with these relationships given the low number of samples, which prevents drawing definitive conclusions.

On the other hand, two of the study reaches with the longest dry phases (Llobregat and Fluvià) lacked water in the HZ, preventing invertebrates from finding refuge in the shallow hyporheic sediments that we sampled, or forcing invertebrate to migrate into deeper sediments find refuge (Clinton et al. 1996). The effectiveness of most resistance strategies decreases with an increase in dry-phase harshness, influenced by the presence of water in the HZ or isolated pools, or moisture in the streambed sediment (Bogan et al. 2017). With extended dry phases and water loss, only few invertebrates are adapted to such harsh conditions (Fritz and Dodds 2004). For instance, many invertebrate seedbank taxa, which have various desiccation-tolerant life stages (e.g., eggs, juveniles), can persist during moderate-intensity dry phases, but as intensity increases, only taxa with cocoons and housing against desiccation can survive (Crabot et al. 2021a). Consequently, extended, severe dry phases can significantly alter aquatic invertebrate community composition (Doretto et al. 2018; Chanut et al. 2022).

Conclusions and prospects for future research

Further research is required to extend our understanding of the invertebrate traits associated with resistance and to evaluate the impact of dry phases on the effectiveness of resistance strategies (Stubbington and Datry 2013; DelVecchia et al. 2022). Our results showed that the taxa within hyporheic refuges and invertebrate seedbanks constituted up to 40% and 16%, respectively, of benthic invertebrate taxa. Additionally, a similar abundance of traits to face with the dry phase was observed across all assemblage types, suggesting a biota adapted to seasonal drying events in Mediterranean streams. Ongoing climate change, as well as human activities including water abstraction, are intensifying the frequency and duration of stream drying (Datry et al. 2018). This escalation may compromise the availability of water necessary to sustain the HZ and to maintain adequate moisture levels to support life in streambed sediments. In light of these challenges, freshwater management strategies should aim to ensure a sufficient supply of water to preserve aquatic biodiversity and the integrity of their recovery mechanisms during dry phases in naturally intermittent streams.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00027-023-01034-x.

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Author contributions AV. Main author. She contributed substantially to the study's conception, data acquisition (field and experimental designs, field samplings, experiment execution, sample processing), data analysis, writing the original draft of the manuscript, edited, approved, and submitted it. RAR. She contributed substantially to the data acquisition (field sampling), reviewing data analysis, reviewing the manuscript, and approved it. MM. She contributed substantially to the study's conception, supervision, data acquisition (field and experimental designs, field samplings), reviewing data analysis, reviewing the manuscript and approved it. IM. She contributed substantially to the study's conception, data acquisition (field and experimental designs, field samplings), reviewing data analysis, drafting and reviewing the manuscript, and approved it. Funding acquisition.

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Data availability The invertebrate data can be found in the Supplementary Information (Table S4). Two trait databases are also available: one (Sarremejane et al. 2020) in the data repository Figshare (https://doi.org/https://doi.org/10.6084/m9.figshare.c.5000633), and the other (Múrria et al. 2020) in the Supplementary Information of the paper.

Declarations

Conflict of interest This work was funded through projects CGL2017-88640-C2-2-R and PID2020-115708RB-C21 funded by MCIN/AEI/https://doi.org/10.13039/501100011033. A.V. received a predoctoral grant PRE2018-084817 (FPI). R.A.-R. received a "Margarita Salas" postdoctoral grant from the Spanish Ministry of Universities and the Next Generation EU—Recovery, Transformation and Resilience Plan. All authors agree with the content of the manuscript, approve its submission for publication, and declare no conflicts of interest.

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Contrary effects of flow intermittence and land uses on organic matter decomposition in a Mediterranean river basin

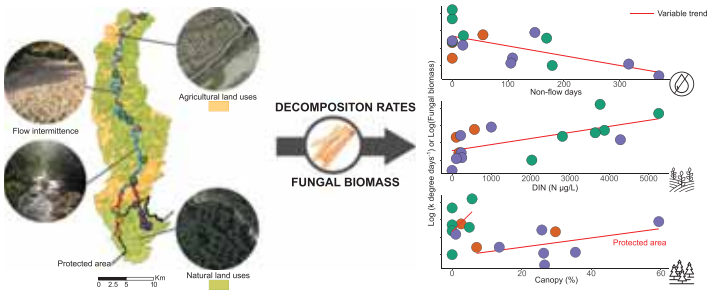
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HIGHLIGHTS

- Intermittent rivers are characterized by high variability in water connectivity.
- Organic matter processing was related to flow intermittence intensity and land uses.
- Negative effect of intermittence was counteracted by agriculture and canopy cover.
- These results complement our understanding of OM dynamics in intermittent rivers.

GRAPHICAL ABSTRACT



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ABSTRACT

Flow interruption in intermittent rivers (IRs) generates a mosaic of terrestrial and aquatic habitats across the river network affecting ecosystem processes, as organic matter (OM) decomposition. Water use for farming in arid and semi-arid climates intensifies the dry conditions and affects local river characteristics. In that way, flow intermittence and the distribution of land uses may affect the OM processing along the river. To understand the role of IRs in global OM dynamics and how global change affecting water flow regimes determines these dynamics, it is important to estimate OM-processing rates at a basin scale. The aim of this study was to evaluate the effect of the intensity of flow intermittence on OM processing, and how this effect was modulated by local environmental factors related to land uses across a Mediterranean river basin. To do this, wood decomposition (mass loss and fungal biomass) was selected as a functional indicator. Drying duration and frequency were measured to characterize flow intermittence in different reaches along the river, as well as local environmental factors. Linear models stablished the role of factors on decomposition. The results showed that differences in decomposition rates across the river network were negatively related to the duration of flow interruption. Dissolved inorganic nitrogen associated with agriculture counteracted the negative effect of intermittence on mass loss (increasing by up to three times); but with a higher duration of dry conditions, its effect was insignificant. An increase of 20% of canopy (higher in natural areas) resulted in increases of up to 5% of mass loss. Overall, our study is relevant to understanding the interaction between flow intermittence and land uses on OM processing, especially considering the intensification of flow intermittence and its increased distribution to other regions, which is expected to be a consequence of climate warming and human activities.
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1. Introduction

Intermittent rivers (IRs) are characterized by periods of flow cessation and are distributed across the world. Flow intermittence in IRs can be natural and/or induced by human impacts, such as water extraction, flow regulation, changes in land use, or climate change (Steward et al., 2012). Flow cessation implies the disruption of hydrological connectivity in one or more spatial dimensions (longitudinal, lateral and/or vertical) under the hierarchy of the time dimension that can reduce or extend the duration of flow cessation (Ward, 1989; Boulton et al., 2017). At the river basin scale, this variability results in a mosaic of terrestrial and aquatic habitats constantly shifting as a consequence of flow contraction and resumption (Datry et al., 2014) and contributes differentially to the processing of organic matter (OM). As the duration of the dry conditions and rewetting periods is a key factor in controlling microbial activity and OM decomposition (Foulquier et al., 2015), this spatial organization of habitats across the basin jointly with the intensity of temporality will determine the annual OM budget in IR networks, which represent more than half of global river networks (Messager et al., 2021). To obtain insights into the role of IRs in global OM dynamics and how climate change and other factors affecting flow regimes determine these dynamics, it is important to estimate differences in OM-processing rates across the basin in IRs, including different habitats and conditions.

An increase in agricultural practice intensification in recent decades has generated large impacts on freshwater ecosystems, such as water nutrient enrichment, especially inorganic N and P concentrations (Paul et al., 2006). In addition, agriculture is the economic sector with the highest water demand, and 40.4% of the total water use in Europe in 2015 was for cultivation practices (EEA, 2018). In water-limited areas, such as in the Mediterranean region, the farming of crops has changed from rainfed to irrigated agriculture with higher water consumption. As a consequence, in Mediterranean regions, where IRs are the most common fluvial ecosystems due to their natural flow regimes, freshwater demand has increased mainly in summer when the water flow is the lowest (García-Ruiz et al., 2011), intensifying dry conditions and flow disconnection in the basin. Land for agricultural uses also modifies stream geomorphology, riparian canopy and hydrochemistry (e.g., higher nutrient concentration and presence of pollutants), and consequently, resulting effects are expected on community diversity and ecosystem functioning (Cooper et al., 2013). Knowledge about how these effects interact with flow intermittence is still limited mainly at basin scale where these pressures change spatially.

OM decomposition is a key process in stream ecosystems and represents an important source of carbon and energy for stream food webs (Tank et al., 2010); therefore, it has been suggested as an indicator of ecosystem functioning (Young et al., 2008). OM decomposition is a result of the interaction between several abiotic and biotic factors. The main biological drivers of stream OM decomposition are microbial decomposers (fungi and bacteria) and invertebrate shredders. In the first stages, aquatic hyphomycetes are the first colonizers producing detritus rich in nutrients and transforming leaf litter into a more palatable resource for shredders (Bärlocher, 1992; Gessner et al., 2010). The decomposition process is also affected by environmental factors, such as temperature (Geraldes et al., 2012), dissolved nutrients (Menéndez et al., 2011), pH (Kok and Van der Velde, 1994) or flow regimes (Martínez et al., 2015). For instance, increased inorganic N and P concentrations stimulate the activity of aquatic hyphomycetes (Sridhar and Bärlocher, 2000; Menéndez et al., 2011), particularly for low-quality substrates (i.e., low nutrients and high lignin content) (Ferreira et al., 2006). In addition, the duration of flow interruption affects fungal activity as a result of the transition between aquatic and terrestrial habitats but fungal activity recovers when flow resumes (Mora-Gómez et al., 2018). Traditionally, OM decomposition was measured using the mass loss of leaf litter bags, which can be variable depending on litter quality because it has a high variability in chemical composition (Lecerf and Chauvet, 2008). Nevertheless, several authors have proposed using alternative standardized substrates, which are less variable in their chemical composition (Tiegs et al., 2007; Young et al., 2008). One of these proposals is wooden sticks (Díez et al., 2002). Although wood decomposition is considered a slow process due to its recalcitrant nature, wooden sticks are small pieces with a high surface-to-volume ratio, which favours their decomposition (Arroita et al., 2012). In addition, wood decomposition responds in the same way to environmental factors as leaf decomposition (Gulis et al., 2004).

Studies at the basin scale have important implications for ecosystem services and functioning and, especially, for water resource management (Allan and Johnson, 1997; Elosegi and Sabater, 2013). Previous studies have shown that at this scale, the variability of OM decomposition depends especially on local factors, such as hydromorphological alterations (e.g., flow regulation) (Abril et al., 2015), land uses (Paul et al., 2006; Tonin et al., 2018) or dissolved nutrients (Molinero et al., 1996). For instance, Paul et al. (2006) analysed the effect of different catchment land uses on leaf decomposition and found that agricultural and urban land uses enhance leaf litter decomposition as a consequence of water nutrient enrichment, especially phosphorous. In the same way, Abril et al. (2015), identified a unimodal distribution of decay rates related to total agricultural land use. Aristi et al. (2012) also found a hump-shaped relationship between decomposition rates and phosphorous related to human activities in permanent reaches of four Mediterranean basins on the Iberian Peninsula. However, there is little knowledge about what happens at the basin scale in IRs considering spatial and temporal variations in flow, especially in understanding the interactions between natural flow intermittence and human stressors, such as nutrient addition (Von Schiller et al., 2017).

The aim of this study is to evaluate the effect of the intensity of flow intermittence during a hydrological year on OM decomposition and how it is modulated by land uses at a river basin scale. To accomplish this objective, the decomposition rates and fungal biomass of wood sticks incubated in 16 sites along a small Mediterranean river are analysed in relation to flow intermittence descriptors and local environmental parameters. Part of the studied basin is located in a protected area conserving the natural vegetation; the other part is characterized by land used for agriculture, whereas urban uses were incidental. We hypothesize that a higher intensity (duration and frequency) of intermittence will negatively affect OM decomposition rates and fungal biomass. However, as agricultural activities can increase water nutrient availability to the microbial community, enhancing its activity and biomass accrual, the negative effects of flow intermittence will be reduced in those reaches where the effect of agriculture is present. This study examines at river basin scale, the spatial variation in the quantity of OM processed and relates it to differences in flow patterns (from permanent reaches to ephemeral) and land uses (agricultural and natural uses).

2. Methods

2.1. Study area

This study was conducted in the catchment of the Algars River, which flows into the Matarranya River, a tributary of the Ebro River, located in the northeastern part of the Iberian Peninsula (Fig. 1). The total area of the catchment is 405 km^2, and the mainstream is 70 km in length. Algars headwaters are divided into two streams, Estrets and Algars, located in the natural park of Els Ports. The climate is typically Mediterranean characterized by scarce precipitation concentrated in spring and autumn with drier and warmer summers. The main land uses were extensive agriculture (44.6% of the total basin, mainly olive groves, fruit trees and vineyards), and natural vegetation (55.3%, mainly coniferous forests, bare rocks, sclerophyllous vegetation and transitional woodland-shrub) while urban land uses were incidental (<0.45%) (© European Union, Copernicus Land Monitoring Service 2018, European Environment Agency (EEA)). We selected 16 sites

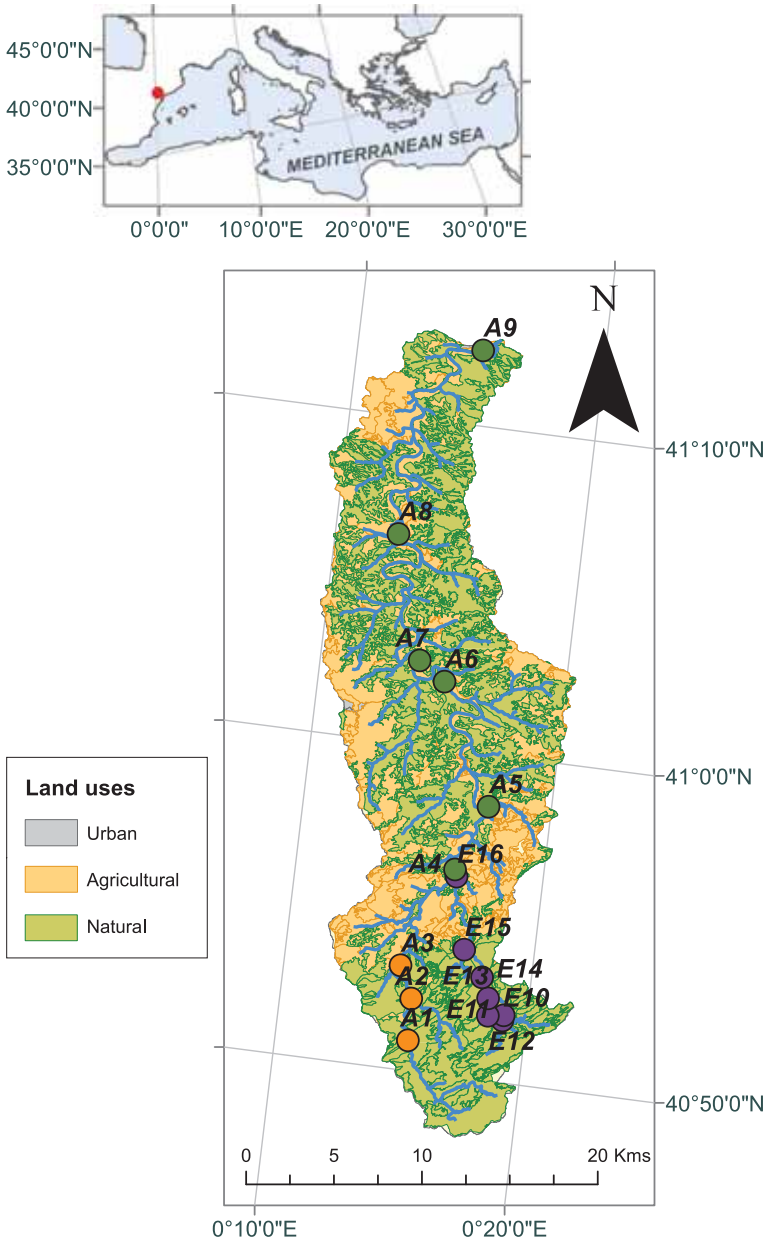


Fig. 1. Location of Algars basin (NE Iberian Peninsula) in the Mediterranean region and land uses distribution in the river basin. Natural land-uses are in green, agricultural land-uses are in orange and urban land-uses in grey. Dots indicate the location of study sites. Purple dots correspond to Estrets stream sites, orange dots correspond to Algars stream sites before the confluence, and green dots correspond to sites on the Algars stream after the confluence.

across the catchment, 7 sites on the Estrets stream, 3 sites on the Algars headwater stream before the confluence with the Estrets and 6 sites on the Algars mainstream after the confluence (Fig. 1). The study was conducted during a hydrological year (November 2018 to November 2019). During this period, the accumulated precipitation in the basin was 368.9 mm, and the mean temperature was 15.1 °C, with a maximum temperature of 40.6 °C at the end of June and a minimum temperature of −4 °C in January (Meteorological Service of Catalonia, METEOCAT).

2.2. Stream flow intermittence

To characterize flow intermittence, two variables were calculated. The total non-flow days, as a measure of the duration of intermittence, and the total times that flow was interrupted, as a measure of the frequency of intermittence. Both were calculated at each site using the water level and daily streambed temperature variation as an indicator of water presence, recorded every hour during the year with leveloggers

(Solinst Levelogger Edge, full-scale reading accuracy of 0.05%) placed on the streambed (Constantz et al., 2001). To correct the recorded data, atmospheric pressure variations from barologgers (Solinst Barologger, full-scale reading accuracy of 0.05%) installed at the riparian zone at each site were used.

2.3. Environmental parameters

During the study period, water physical and chemical parameters were seasonally (November 2018, February 2019, May 2019 and August 2019) measured at each site (Tables 1 & S1). A portable probe (YSI Professional Plus Multiparameter Instrument, USA) was used in situ for electric conductivity, water temperature, water dissolved oxygen and pH (± 1 μs cm^{-1}, ± 0.1 °C, ± 0.1 mg L^{-1} and ± 0.005 pH, respectively). To characterize water nutrient concentrations, three water samples were filtered through glass fibre filters (0.7-μm pore size; Whatman GF/F, Germany) into prewashed polyethylene containers, transported to the laboratory and stored at 4 °C in the dark until analysis. Water samples were analysed by ionic chromatography ($\pm 2.8\%$ at 1 ppm; IC5000, DIONEX, USA) to obtain concentrations of magnesium (Mg^{+2}), calcium (Ca^{+2}) and dissolved nitrogen (N) in nitrite form (NO_2^-), nitrate form (NO_3^-) and ammonium form (NH_4^+). The sum of dissolved N forms was expressed as DIN. Dissolved organic carbon (DOC) was measured by a TOC analyser (TOC-V CSH, Shimadzu Corporation, Japan). The concentration of soluble reactive phosphorus (SRP) was determined by a colorimetrically discrete analyser (Alliance Instruments Smartchem 140, AMS, France).

To characterize land uses, a sub-basin at each site was delineated from a digital elevation model at a 25-m resolution by computing the flow direction and using a watershed tool with geospatial-processing software (ArcMap 10, ArcGIS, USA). The percentages of simplified land-use cover (urban, natural and agricultural land uses) adapted from Corine Land Cover 2018 were calculated at each site.

The average of canopy cover percentage at each site was calculated using a spherical densitometer (Lemmon, 1956), taking four measures (upstream, downstream, right side and left side of the site) at three points of each site.

2.4. Decomposition rates and fungal biomass

To calculate decomposition rates, 10 tongue depressor sticks of Canadian poplar wood (*Populus x canadensis*) (15 × 2 × 0.2 cm) (Arroita et al., 2012) were placed in the riverbed at each site in November 2018. All wood sticks were previously marked, oven-dried (70 °C, 72 h) and weighed. Five wood sticks were collected after 90 days, and the other five were collected after one year of incubation. Sticks were placed in zip-lock bags and transported to the laboratory in refrigerated containers. To avoid ergosterol degradation and changes in weight, wood sticks were processed immediately in the laboratory. First, wood sticks were brushed to remove adhered material and washed with distilled water. Later, an aliquot of 1 cm of each stick was cut and frozen at −80 °C for later determination of ergosterol concentration as a proxy of fungal biomass (Gessner, 2005). The remaining part of each wood stick was dried (70 °C, 72 h), weighed and summed to the fraction of the frozen aliquot to measure ergosterol (see below). Then, another 1-cm-long aliquot of each wood stick was cut and incinerated (500 °C, 5 h) to remove inorganic components and to determine the AFDM[6]. The initial AFDM was determined from an extra set of 20 sticks. This set was also transported into the field but not placed in the river and returned to the laboratory, which was processed as described above to calculate a conversion factor between the initial air-dry mass and the initial AFDM, considering manipulation losses.

To determine ergosterol concentration, frozen aliquots of each wood stick were lyophilized and weighed. Lipid extraction and saponification were performed using 0.14 M KOH methanol (8 g L^{-1}) in a shaking bath at 80 °C for 30 min. To purify lipid extractions, solid-phase extraction cartridges were used (Waters Sep-Pak® Vac RC, 500 mg tC18 cartridges, Waters Corp, Milford, MA, USA), and ergosterol was eluted using isopropanol. High-pressure liquid chromatography (HPLC; Jasco HPLC system, USA) was used at 282 nm to detect and quantify ergosterol using a Gemini-NX 5 μm C18 250 × 4.6 mm column (Phenomenex, UK). The ergosterol measurement was converted into fungal biomass using a conversion factor of 5.5 mg of ergosterol per gram of fungal mycelium (Gessner and Chauvet, 1993). The results were expressed as mg of fungal biomass per gram of dry mass.

Decomposition rates were calculated following the negative exponential equation $M_t = M_0 \cdot e^{-kt}$, where M_0 is the initial percentage of AFDM, M_t is the remaining AFDM at time t, k is the decay rate, and time t was replaced by the mean daily temperatures accumulated to express decay rates in degree days (dd^{-1}), i.e., in terms of accumulated heat (Stout, 1989). The mean daily temperatures were obtained from leveloggers.

2.5. Data analysis

To explore the environmental variables jointly and their relationships with sites, Principal Components Analysis (PCA) was performed. All environmental variables, including flow intermittence descriptors, were used. This analysis will also allow us to assess the relationship between variables.

To analyse how flow intermittence and environmental characteristics affected the decomposition rates, automated model selection for the linear regression model was performed using the R package MuMIn (Barton, 2009) to select the best combination of all predictor variables based on AICc (Akaike Information Criterion corrected version for small samples). To assess collinearity between explanatory variables, pairwise Pearson correlations and the variance inflator factor (vifstep of usdm R Package) (Feld et al., 2016) were previously estimated. Therefore, agricultural land uses (highly correlated with DIN[3] concentration), conductivity (correlated with Ca and DOC) and Mg (correlated with Ca) were discarded (Table S2). Then, the final set of explanatory variables tested in the automated model included the annual means of seasonal variables (DIN, Ca and DOC), flow intermittence variables (non-flow periods and non-flow days) and basin descriptors (canopy).

To analyse the effects of flow intermittence and environmental characteristics on fungal biomass, automated model selection for the mixed linear model was performed using the R package MuMIn (Barton, 2009) to select the best combination of predictors. Fungal biomass values at two sampling times (90 and 365 days) were used considering time as a fixed effect factor, while site was considered a random effect factor. For these analyses, the averages of seasonal variables (DIN, Ca, Mg, DOC, water temperature and conductivity) and flow intermittence variables (non-flow periods and non-flow days) were calculated at 90 and 365 days (Table S2). To assess predictor collinearity, the same previous methodology explained above was conducted. Here, DIN, non-flow days, Ca, water temperature, conductivity and canopy were included in the analysis.

To relate fungal biomass to decomposition rates, linear regression was performed.

The linear model assumptions were assessed and verified for all models performed (Poole and O'Farrell, 1971). The distribution of all variables was explored before the statistical analysis. All explanatory variables, except non-flow periods, were squared-root-transformed. Decomposition rates (k_{dd}) and fungal biomass were log-transformed. All variables were finally Z-standardized (mean = 0, SD = 1) to facilitate model coefficient comparison and avoid the influence of the measurement units in PCA. All statistical analyses were performed using R software (R Core Team, 2020).

3. Results

3.1. Environmental characteristics

The Algars river presented permanent, intermittent and dry sites across the basin (Table 1). Intermittent sites presented great variability in intermittence intensity in the studied period. Specifically, for intermittent sites, non-flow days varied between 19 and 315 days, with a mean of 124 days, and non-flow periods varied between 1 and 4, with a mean of 1.8. Water characteristics were variable across sites (Tables 1 & S1). Magnesium (4.5–13.4 mg L^{-1}), calcium (30.0–68.7 mg L^{-1}), DOC (2.9–101.0 mg L^{-1}), and conductivity (297.2–1086.9 μS cm^{-1}) showed a similar trend, increasing downstream except in the Estrets stream. The percentage of dissolved oxygen presented values between 66.1 and 107.0, where E12 had the lowest value and E13 the highest (Table 1). The pH varied between 7.9 and 9.0. Dissolved inorganic nitrogen (DIN) was used as representative of all nitrogen forms and varied between 105.3 and 5261.5 μg/L. The main dissolved nitrogen form was nitrate and was related to agricultural practices in each subbasin. For instance, the concentration of DIN at site A4 was the highest, which was also the site with the highest percentage of agricultural land use (73.3%). Canopy cover varied between 0 and 59%, which was related to headwater sites and smaller width of the streambed.

The first two components of PCA with the environmental variables explained almost 70% of the total variance. (Table S3). Specifically, PC1 explained 43.31%, while PC2 explained 26.08% (Fig. 2). PC1 indicated environmental characteristics and separated headwater sites (Estrets and Algars headwater streams) characterized by lower conductivity and a higher percentage of canopy than downstream sites (Algars after the confluence). PC2 separated sites according to flow intermittence measures and agricultural land uses (Table S4). However, intermittent sites with low non-flow days (E16, A3 and A6) were situated next to permanent sites because these sites were characterized by low canopy cover and high DIN concentrations. On the other hand, permanent sites A4, A5 and A7 were characterized by high DIN concentrations and a great proportion of agricultural land uses, while sites E12, A1 and A2 were permanent but with a high percentage of natural land uses and low DIN concentrations.

3.2. Decomposition rates

Decomposition rates (k_{dd}) varied between $9.2 \cdot 10^{-6}$ and $4.1 \cdot 10^{-4}$ dd^{-1} (Fig. 3A; Table S5). The highest values corresponded to A4 and A5 ($2.4 \cdot 10^{-4}$ and $4.1 \cdot 10^{-4}$, respectively), sites located downstream, permanent sites and sites with the highest DIN concentration. The lowest values corresponded to E11, E15 and A8 ($9.2 \cdot 10^{-6}$, $1.8 \cdot 10^{-5}$ and $1.7 \cdot 10^{-5}$, respectively), sites with the highest duration of intermittence (370, 316 and 179 days, respectively). The results of model selection showed that k_{dd} was associated with DIN, canopy and non-flow days (adjusted $R^2 = 0.58$; $F_{3,11} = 7.35$; p-value $= 0.006$). All variables were significant (Table S6). DIN and canopy had a positive coefficient, which implies an increase in k_{dd} with higher values of DIN and canopy. However, non-flow days had a negative coefficient, which indicates a decrease in k_{dd} with higher values of non-flow days.

The percentage of AFDM lost increased between 15 and 55% due to the DIN effect (Fig. 4) depending on the hydrological regime. For instance, permanent sites with low DIN concentrations (A1, A2 and E12) had AFDM losses of 12.2%, 18.0% and 20.1%, respectively, while A4 and A5, permanent sites but with 30 times more DIN, had the highest AFDM losses (56.8% and 66.8%, respectively). In intermittent reaches, sites with a high DIN (E10, A6 and A9) had a higher AFDM loss (39.7%, 27.6% and 24.9%, respectively) than sites with a low DIN (E13, E14 and E15 with 13.0%, 11.1% and 6.9%, respectively). Then, the effect of non-flow days was clear on E12, E13 and E14 with low DIN concentration values, and AFDM loss decreased almost 20% with an increase in non-flow days. However, E11, E15 and A8, with different DIN concentrations, had a similar AFDM loss because the severity of intermittence was the highest at these sites. In addition, an increase of 20% of canopy meant increases next to 5% of AFDM lost. For example, A1 and A2 were permanent sites with similar DIN concentrations and 7.0% and 29.7% of the canopy, respectively. A2 presented 6% more AFDM loss than A1. Another example was intermittent reaches E10 and E16: E16 had 76.7% higher DIN concentrations, 129 non-flow days less and 58.3% less canopy cover than E10, but E10 had 19.1% more AFDM loss than E16.

3.3. Fungal biomass

Fungal biomass associated with wood litter varied between 2.8 and 294.8 μg/g AFDM (Fig. 3B; Table S7). In general, the one-year fungal biomass presented greater variability and values than that observed after

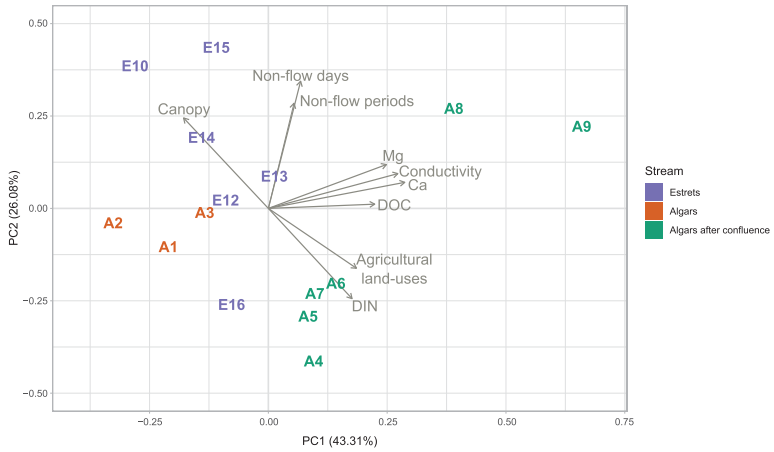


Fig. 2. PCA biplot representation using PC1 (43.3% variability) and PC2 (26.1% variability). Sites are represented by their names and with colours of their respective streams (purple for the Estrets stream, orange for the Algars stream before the confluence, and green for the Algars sites after the confluence). The grey arrows represent the component weights and allow us to understand the relationship between variables and principal components.

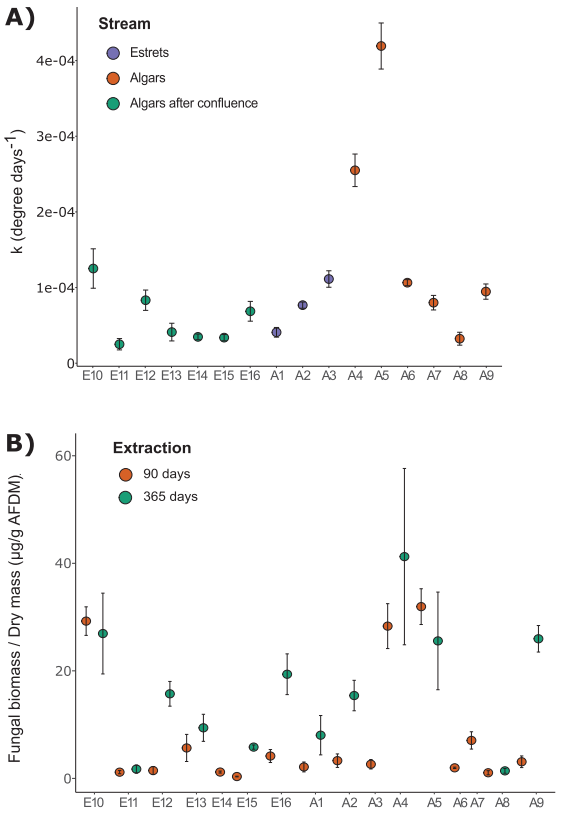


Fig. 3. A) Mean plot of decomposition rates at all study sites of the Algars river basin. Decomposition rates are in degree days^{-1}. Colours correspond to the respective streams of each site (purple for the Estrets stream, orange for the Algars stream before the confluence, and green for the Algars sites after the confluence). B) Mean plot of fungal biomass at each site and at each extraction. Orange colour corresponds to the 90-day extraction, and green colour corresponds to the 365-day extraction. All dots represent the means, while the bars represent standard error.

three months of incubation. A linear and positive relationship was found between the logarithm of decomposition rate and fungal biomass (adjusted $R^2 = 0.55$; $F_{2,25} = 17.64$; p-value <0.0001; Table S8; Fig. S1).

The model obtained with model selection showed that the fungal biomass was related to DIN, canopy, non-flow days and extraction days (conditional $R^2 = 0.70$). DIN, estimated parameters of canopy cover and extraction days were significant and showed a positive coefficient (Table S9), which implies an increase in fungal biomass related to incubation time at higher DIN concentrations and canopy cover. The estimated parameter of non-flow days was marginally significant (p-value = 0.069) and had a negative coefficient, indicating a decrease in fungal biomass with an increase in non-flow days.

4. Discussion

The distribution of land uses in the basin reveals interactive effects with flow intermittence on OM decomposition. We hypothesized that an increase in intermittence intensity negatively affected the decomposition rates in the study basin. Our results confirmed this prediction, and the sites with more than 170 days of flow cessation showed the lowest decomposition rates. Non-flow days were one of the predictors of the decomposition dynamics selected by the linear model with a negative effect. This effect was counteracted by the presence of nutrients (DIN) coming mainly from agricultural activity and, with a lower intensity, from canopy cover, which was not expected in our initial hypothesis.

In natural reaches (without anthropogenic activities), intermittence reduced the processing of OM (measured as AFDM) by a mean of 14.9% in comparison with permanent sites, and this reduction was higher with an increase in intermittence duration, as previous studies found (Corti et al., 2011; Datry et al., 2011). As flow fragmentation is variable along the river, spatial and temporal habitat heterogeneity creates different ecological conditions that result in a diverse decomposition process in accordance with the prevailing environmental conditions (Abril et al., 2016). For instance, in dry streambeds, such as site E11, the decomposition process is terrestrial with lower mass losses because terrestrial detritivores are scarce and microbial activity declines (Maamri et al., 1997; Corti et al., 2011). Thus, OM decomposition is faster in aquatic systems than in terrestrial systems due to enhanced leaching, microbial metabolism, and aquatic invertebrate activity (Mora-Gómez et al., 2020).

Intermittence intensity was measured by non-flow days and the number of dry periods, but only non-flow days were a selected predictor for decomposition rates and fungal biomass. The first variable could be considered a measure of the duration of the flow interruption, while the second could be considered a measure of its frequency (Langhans and Tockner, 2006). Coinciding with our results, previous studies found that the duration of dry periods had more influence on OM decomposition than their frequency because the activity of aquatic decomposers decreased with a reduction in flow, but they quickly recovered their activity after rewetting (Pohlon et al., 2013; Foulquier et al., 2015; Niyogi et al., 2020), especially microbial decomposers, considering that aquatic invertebrates take slightly longer to recolonize the reach (Corti et al., 2011).

In Mediterranean rivers, the drying phase is a scaled and prolonged process during the summer period, while the resumption of flow is usually faster across the network during autumn (Vazquez et al., 2013; Boulton et al., 2017). Our results showed an increase in fungal biomass with time, which suggested a fast recovery of fungi after autumnal rewetting. However, during the drying phase, aquatic decomposer communities were affected by changes in environmental conditions in different ways. For instance, isolated pools characterized by a decrease in water flow and low oxygen and detritus accumulation were harsh habitats for fungi (Canhoto et al., 2016), while these conditions did not affect bacteria. Abril et al. (2016) found a decrease in fungal biomass in isolated pools during the drying phase compared with running waters, while bacterial biomass did not show differences between these habitats. In any case, the presence of water determines the continuity of the processing of OM by microbial assemblages, and when water disappears, this process practically stops. Even so, previous studies showed that fungi could be less sensitive to severe drought than bacteria (Maamri et al., 2001; Duarte et al., 2017). In our study, the close relationship between decomposition rates and fungal biomass would suggest that fungi were the main driver of wood decomposition and that their responses to flow variability (although marginally significant in the model) could explain differences in OM processing in the studied basin.

On the other hand, and as we hypothesized, agricultural land uses increased water nutrient enrichment in streams, which positively affected OM decomposition rates. A positive effect of water nutrient enrichment was also observed in relation to fungal biomass. For instance, Abril et al. (2015) identified a unimodal distribution of decay rates related to total agricultural land use in summer in a Mediterranean basin, when temperature and nutrient concentrations increased. In addition, they found that high order reaches presented lower decay rates and less variability between winter and summer than low order reaches, where agricultural practises had a greater presence. These results are consistent with previous studies (Stelzer et al., 2003; Gulis et al., 2004). Fungi have the capability to use inorganic nutrients from water, especially when they colonize a poor-quality substrate, such as

Table 1
Land uses, flow intermittence, canopy cover and chemical water characteristics in the studied reaches. Percentages of land use cover refer to the total sub-basin area associated with each site. Urb. = urban, Agr. = agricultural, and Nat. = natural land uses. DOC = dissolved organic carbon. DIN = dissolved inorganic nitrogen. Values (Mean ± SE) are the mean of the four field campaigns. NA: only one value was available to calculate the mean. Site E11 was always dry when we went to the field.

Site	Catchment land–uses (%)			Flow intermittence				Canopy cover (%)	Chemical water characteristics						
	Urb.	Agr.	Nat.	Non-flow periods	Flow periods	Non-flow days	Flow days		Mg (mg Mg/L)	Ca (mg Ca/L)	DOC (mg C/L)	DIN (μg N/L)	Conductivity (μS/cm)	DO (%)	pH
E10	0	33.41	66.59	4	3	148	222	59.4 ± 6.4	4.6 ± 4.3	30.5 ± 9.0	22.1 ± 7.2	999.8 ± 422.6	311.3 ± 20.2	81.4 ± 6.2	8.5 ± 0.1
E11	0	0	100	0	0	370	0	26.6 ± 3.9	–	–	–	–	–	–	–
E12	0	0	100	0	0	0	370	25.8 ± 5.3	7.0 ± 6.5	43.4 ± 11.1	54.0 ± 18.2	218.8 ± 14.8	522.5 ± 36	65.2 ± 1.3	7.9 ± 0.2
E13	0	33.41	66.59	1	1	108	262	13.5 ± 1.1	7.9 ± 7.4	40.8 ± 8.7	56.2 ± 27.3	231.7 ± 46.9	489.3 ± 34.9	107.0 ± 4.4	8.8 ± 0.3
E14	0	33.41	66.59	2	2	105	265	35.4 ± 2.6	6.2 ± 5.7	34.5 ± 8.2	41.7 ± 20.1	247.7 ± 74.1	414.2 ± 47.3	87.3 ± 3.7	8.7 ± 0.2
E15	0	0.21	99.79	1	1	316	54	26.3 ± 4.6	12.2 ± NA	43.9 ± NA	2.9 ± NA	109.0 ± NA	297.2 ± 43.9	85.2 ± 12.0	8.6 ± 0.2
E16	0	33.41	66.59	1	1	19	351	1.0 ± 0.4	5.0 ± 4.3	30.0 ± 2.4	32.6 ± 11.4	4287.0 ± 1941.9	420.6 ± 18.6	91.8 ± 4.4	8.8 ± 0.1
A1	0	3.10	96.90	0	0	0	370	7.0 ± 2.9	5.8 ± 5.4	35.9 ± 9.1	30.0 ± 9.9	177.5 ± 52.9	360.4 ± 18.5	95.3 ± 3.0	9 ± 0.1
A2	0	3.10	96.90	0	0	0	370	29.7 ± 2.5	4.8 ± 4.4	31.1 ± 9.6	25.6 ± 8.8	105.3 ± 28.1	325 ± 27.3	86.4 ± 3.9	8.9 ± 0.1
A3	0	3.10	96.90	1	1	55	315	2.6 ± 2.3	6.6 ± 6.0	37.3 ± 10.0	34.4 ± 11.0	569.8 ± 359.8	395.3 ± 32.1	87.8 ± 4.2	8.3 ± 0.6
A4	0	73.33	26.67	0	0	0	370	0.0 ± 0.0	7.2 ± 6.2	38.9 ± 9.7	34.9 ± 11.2	5261.5 ± 1291.5	434.8 ± 27.6	90.9 ± 5.9	8.9 ± 0.1
A5	0.01	57.57	42.42	0	0	0	370	5.7 ± 2.5	7.5 ± 6.0	45.3 ± 10.9	40.8 ± 13.2	3770.3 ± 1461.9	442.5 ± 35.6	100.8 ± 4.5	9.1 ± 0.1
A6	0.01	57.57	42.41	1	1	20	350	0.0 ± 0.0	9.9 ± 8.2	46.5 ± 12.4	33.9 ± 15.9	3881.0 ± 1377.5	427.4 ± 58.7	100.0 ± 6.2	9 ± 0.1
A7	0.45	47.79	51.76	0	0	0	370	0.0 ± 0.0	10.4 ± 8.7	48.6 ± 12.3	32.2 ± 14.9	2810.0 ± 1413.3	470.1 ± 31.9	83.0 ± 10.9	8.8 ± 0.1
A8	0.45	47.79	51.76	3	2	179	191	0.0 ± 0.0	11.8 ± 9.9	55.7 ± 10.8	44.7 ± 21.1	2031.3 ± 1206.0	986.1 ± 473.3	87.0 ± 7.8	8.8 ± 0.3
A9	0.24	46.73	53.02	2	2	169	201	4.9 ± 2.0	13.5 ± 10.0	68.7 ± 8.0	101.0 ± 56.6	3645.3 ± 955.4	1086.9 ± 346.2	81.8 ± 12.8	8.5 ± 0.4

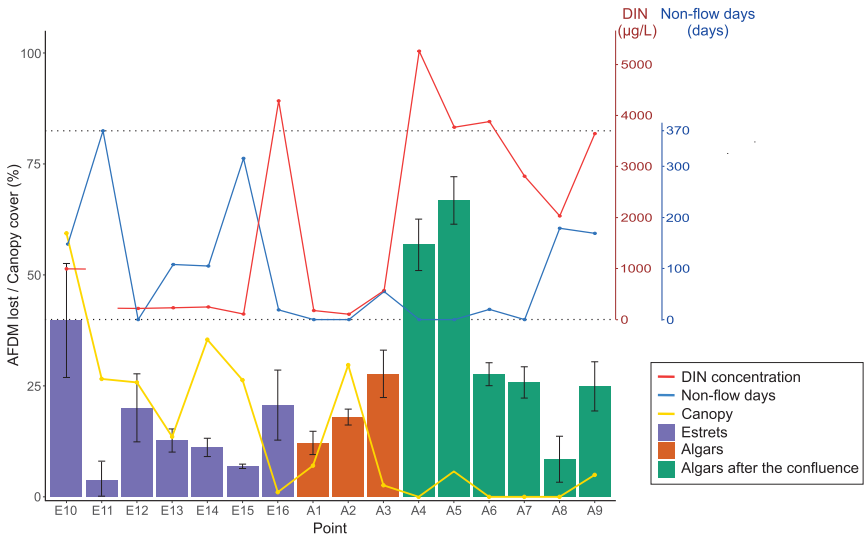


Fig. 4. Barplot of percentage of mean of ash free dry mass (AFDM) lost, filled with colours that correspond to their respective streams (purple for the Estrets stream, orange for the Algars stream before the confluence, and green for the Algars sites after the confluence). The yellow line is the percentage of canopy cover at each site. The blue line corresponds to the total number of non-flow days at each site. The red line is the mean DIN concentration at each site (μg N/L). Vertical bars represent the standard errors.

wood, which is rich in lignin with a high ratio of C:N (Suberkropp, 1998; Sridhar and Bärlocher, 2000; Stelzer et al., 2003; Ferreira et al., 2006). The predominant form of DIN in the study basin was nitrate (Table S1), which is associated with anthropogenic activities, especially with agricultural practices (Lassaletta et al., 2009), and it could cause a significant change in decomposition rates and fungal biomass with small increases (Ferreira et al., 2006).

Our results suggested that DIN concentration modulated the negative effects of the duration of flow intermittence: the presence of DIN favoured OM processing. For instance, at sites with a similar number of non-flow days, the processing of OM was up to three times lower with low DIN concentrations, while the processing of OM when comparing permanent and intermittent reaches was reduced almost two times at sites with high DIN concentrations. However, if the severity of the intermittence increased, the effect of DIN seemed to be insignificant. This interaction between factors existed across the basin, especially at downstream sites, where agricultural practices were more important.

Additionally, our results showed that the percentage of canopy cover also affected decomposition rates and fungal biomass. Canopy cover is related to forestry land uses extending to headwater sites, where fungi are considered the main decomposers of leaf litter and bacteria play a secondary role (Hieber and Gessner, 2002). This could justify the differences found in decomposition rates and fungal biomass at headwater sites with similar durations of intermittency and low DIN concentrations. High canopy cover implies an entry of allochthonous leaf litter, which could stimulate fungal biomass and their activity (Gessner et al., 1999). Canopy cover reduces sunlight incidence, especially ultraviolet radiation (UV), which has direct effects on fungal development (Newsham et al., 1997). The decrease in light availability limits the growth of algal biofilms, reducing competition with fungi for inorganic nutrients (Daufresne and Loreau, 2001). Algal biofilms are also an indirect competitor for fungal decomposers because algae are a more nutritive resource than leaf litter for invertebrates (Tonin et al., 2018). In summary, light affects microbial assemblages in streams, limiting fungal development, favouring algae and having low or no effect on bacteria (Albariño et al., 2008), but other authors have also considered that algae stimulate the presence of bacterial decomposers (Danger et al., 2013), maintaining the processing of OM, especially in downstream sites. All this will have an effect on the processing of OM in streams. For instance, site E16 presented a high light incidence, which explained the presence of a high density of filamentous algae (personal observation), which could be related to the low decomposition rate and fungal biomass observed, even with a high DIN concentration. However, the effect of canopy cover was clear only in headwater reaches, where this factor showed variability, but not downstream, where all sites were open and unshaded.

Fungal biomass explained more than 50% of the decomposition rates in the study basin. Nevertheless, the site with the highest decomposition rates (A5) did not have the highest fungal biomass, and other biotic components affected decomposition processes in the Algars basin. Previously, we mentioned the competition between microbial communities (algae, fungi and bacteria) related to nutrients and light availability, but in addition to this permanent site, we observed a high density of American crabs (*Procambarus clarkii* Girard, 1852), which fragmented the wood sticks, causing mass loss. *Procambarus clarkii* is an invasive species on the Iberian Peninsula with high plasticity to environmental variability (Geiger et al., 2005) but is usually found in downstream reaches with low riparian quality and eutrophication (Maceda-Veiga et al., 2013).

Flow intermittence affects OM decomposition and fungal biomass in the entire basin, but the drying phase is variable across the river network and time, resulting in differences in flow disruption and its duration. The mosaic between terrestrial and aquatic habitats and the duration of flow interruption imply great variability in the quantity of processed OM and the potential for its transport among the habitats, which was not studied here. In addition, land uses and human activities, such as water nutrient enrichment, also affect the decomposition process in the entire basin, but this effect is related to local impacts and their position in the river network. However, as a generalization, agricultural land uses were located on downstream and forested streams on headwater. Even so, local characteristics are important in explaining the differences across the basin in the processing of OM and in the global budget of carbon in receiving downstream waters (Del Campo et al., 2021).

5. Conclusions

This study demonstrated the negative effect of the duration of flow intermittence on OM decomposition, and how interacted with other local environmental factors across the river basin. An increase in the intensity of flow intermittence reduced OM decomposition, but water nutrient enrichment – favoured by agricultural activities – and canopy cover – related to forested headwaters – counteracted this effect. Nutrients artificially accelerate natural OM processing in the study basin and canopy cover also have a positive effect on OM processing. However, if the severity of the intermittence increased, the effect of counteracted factors seemed to be insignificant. Flow intermittence is a natural perturbation in Mediterranean rivers, but its intensification and increase to other regions is expected to be a consequence of climate warming and an increase in freshwater demand. In the current context of global change, it is especially relevant to further investigate the interactions between flow intermittence and other factors on OM processing at the basin scale to incorporate these data into the global carbon dynamics in IRs. Locally, our results will help to preserve natural resources in the study basin, as well as to improve river management, maintain natural uses in headwaters to guarantee the role of riparian forests as a source of OM inputs, limit light and stimulate microbial decomposition, and control nutrient inputs from agricultural downstream areas.

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CRediT authorship contribution statement

A. Viza: Conceptualization, Methodology, Software, Formal analysis, Writing - original draft. **F. Oliva:** Formal analysis, Writing - review & editing. **I. Muñoz:** Conceptualization, Methodology, Writing – review & editing, Supervision, Funding acquisition. **M. Menéndez:** Conceptualization, Methodology, Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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