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D2.4. A report on the existing European meta-community and trait database

Abstract

Drying River Networks (DRN-s) represent more than half of Earth's waterways and because of their fluctuating hydrology have unique physical, chemical, and biological characteristics which reflects in the freshwater metacommunities that inhabit them. DRN-s are one of the most vulnerable ecosystems and due to climate change, drying periods are changing in frequency and duration. DRN-s. Goal of this task is to create a copilation of European freshwater metacommunity data as well as drying resistance and resilience traits of freshwater bacteria, fungi, diatoms, macroinvertebrates and fish.

For this report available data, literature, published and grey literature, as well as expert opinion has been included.

Keywords

Trait, drying, resistance, resilience, DRN

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[1] **Use one of the following codes:**
R=Document, report (excluding the periodic and final reports)
DEM=Demonstrator, pilot, prototype, plan designs
DEC=Websites, patents filing,press & media actions, videos, etc.
OTHER=Software, technical diagram, etc.
ORDP : Open Research Data Pilot

[2] **Use one of the following codes:**
PU=Public, fully open, e.g. web
CO=Confidential, restricted under conditions set out in Model Grant Agreement
CI=Classified, information as referred to in Commission Decision 2001/844/EC.

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Background and rationale

Climate change has a very serious effect on biodiversity and the rise of average temperatures is accompanied by the changes in the precipitation which in turn can increase drought stress (Thuller 2007). Consequences can be seen in natural and artificial environments and as a form of disturbances on habitats which cascade trough biodiversity to ecological functions, and finally to environmental services. As a result of climate change, increasing number of perennial rivers across the globe are becoming intermittent (Datry et. al. 2016), and duration and frequency of drying events is increasing indicating that small freshwaters ecosystems are one of the most vulnerable type of habitats. Anthropogenic pressures on nature grow, and a better understanding of the mechanisms that structure aquatic communities is needed (Santilian et al. 2019). As a result, trait-based approaches are becoming increasingly popular.

The purpose of this report is to list metadata on existing metacommunity data across Europe and to list and describe the drying resistance and resilience traits of bacteria, fungi, diatoms, macroinvertebrates, and fish. Also, the importance and accuracy of traits, given their effect on the individual organism, as well as coverage in the literature will be included trait by trait. Five listed groups represent five different approaches to determination of the traits and understanding of ecosystem functions, as well as give different information regarding their survival of suboptimal environmental conditions.

All present data and trait knowledge is gained from existing literature, published data and direct expert opinion. Literature coverage varies and it will be defined in the following text, traits and definition of their influence is open to scrutiny.

Metadata description:

This part of the document is a description of the compilation of existing meta-community databases in Europe which aims to provide instruction and clarification on the gathered metadata and assembled metadata list. While the Trait database compiles trait information on taxa present in European DRNs, this dataset is a compilation of metadata gathered from easily accessible databases focusing on information across Europe and data regarding taxa presence, flow intermittency patterns, water temperature, and other. The search for this data was conducted along the search for trait data and encountered while accessing relevant databases. Information on the datasets was gained trough literature such as review papers describing a certain point of research or encountered during work with different databases. Datasets are shaped in different formats (e.g. from the perspective of samples, or taxa) and contain different information on habitats, methodology or taxa presence. Although search for species records was avoided and focus was put on community metadata, such information might be found among the provided datasets due to multiple formats which can include valuable information. The dataset DRYvER ST2.2.1 Metadata spreadsheet contains basic metadata on the dataset such as its ID, name, corresponding person for the dataset and their contact as well as website reference and accessibility. It also includes taxonomical, spatial, and temporal information (dates or time frames of sampling and/or taxa presence), methodology used and environmental information on the location if sampling. To get better coverage of the European river flow intermittency patterns and spatio-temporal taxa presence, databases on specific taxa groups are included. Many databases may be lacking in their comprehensiveness of the needed data because of different focuses and aims of the research out of which they were created but still contain valuable information that can be extracted. Since flow intermittency information is rarely included in such datasets (other than the type of habitat where the sample was gathered) the usage of HydroSheds (link: https://www.hydrosheds.org/) data is recommended.

Trait description:

Trait is a term that is broadly used, adjusted to the issue the researcher is trying to resolve and there are functional, effect and response traits (Díaz et al. 2013). Here, we are focusing on functional traits improving resistance and resilience to drying. Functional traits are morphological, biochemical, physiological, structural, phenological, or behavioral characteristics that are expressed in phenotypes of individual organisms and are considered relevant to the response of such organisms to the environment and/or their effects on ecosystem properties (Violle et al. 2007, as cited in Díaz et. al. 2013) It is often used as a synonym to terms such as: characteristic, type, feature and function. The term trait lacks a clear definition but can also be defined as a property of an organism that have a connection to their performance (Kearney et. al. 2021). In this report we use trait as a term to unify the listed synonyms under one and connect it with a function in the environment. In the case of this report, the function is drying resistance, which is the capacity to tolerate, and drying resilience, which is a capacity to avoid and or recover. Using the approach of traits, we can better follow the patterns of succession, understand the mechanisms driving the changes of the community, and as such, predict the changes and influences (e.g., temperature changes and variations) on community diversity and function (Iltis et al. 2019). This approach can also be used to compare different vulnerability of a species to given environmental disturbances based on their traits, as well as be used as an indicating function of habitat state and or quality (Chagon et al. 2013; Smallegange and Berg 2019).

For this deliverable, traits will be divided under four categories: **typology, coding, coverage and importance**. Their purpose is to make traits quantifiable, comparable, and easier to understand and apply. Typology refers to the type of biological traits, such as **morphological, physiological, behavioral, reproductive**. Coding refers to **categorical** (yes/no, 1/0), **numerical or quantifiable** (e.g., 1-10, number of categories is determined per example) and **fuzzy** (hard to define limits, describing the influence, e.g., low, medium, high). Availability of information will be determined from **low coverage** to **high coverage**. And importance refers to how well a trait confers chances of survival to drying (e.g., **low chance of survival, medium chance of survival, high chance of survival**). Contributing/complementing categories are added to the text in form of lists of relative traits, further notes and additional traits. Relative traits represent traits that maybe taken into consideration for functional diversity measures but are not related to drying resistance or resilience (e.g. functional feeding groups, or size of diatoms; both smaller or bigger size respectfully have certain advantages with regards of drying survival). Further notes are not imperative for drying survival but can give insight in certain ecological functions, advantages or disadvantages in drying survival (e.g. gram-positive bacteria have greater chance of drying survival). Additional traits are not aimed solely to describe drying survival but can contribute to it. They can be used to better describe ecosystem functioning (e.g. life history can give information on ecosystem functioning and can also be used as an indicator of drying survival capability).

General databases:

The freshwaterecology.info database was set up for the purposes of the EU funded AQEM project (www.aqem.de) to develop and test an integrated assessment system for the ecological quality of rivers throughout Europe using benthic macro-invertebrates. It is a database that is constantly being updated and can be called a “living document”. It was assembled from the information on the taxa as well as taxa occurrence data within the project partner countries. Since its first upload, the database has been improved and data added. This database will be used as a source of data for diatoms, macroinvertebrates, and fish (Schmidt-Kloiber and Hering 2015).

https://www.freshwaterecology.info/index.php

TraitBank is a part of EOL and it is a “living” database that provides information on traits, interactions, measurements and other (Parr et al. 2014).

https://eol.org/traitbank

GBIF—the Global Biodiversity Information Facility – global database containing datasets on all life forms on Earth

https://www.gbif.org/

Environmental Data Initiative is a platform with the purpose of preserving and distributing environmental data.

https://edirepository.org/

CESTES database is a global database compiled of 80 datasets containing information about species community abundances or presences/absences across multiple sites, species trait information, environmental variables, spatial coordinates of the sampling sites (Jeliazkov et al. 2020).

https://icestes.github.io/database.html

IRBAS database is a database with a purpose of analyzing biological, hydrological and environmental data from drying river networks across the world (Leigh et al. 2017).

https://www6.inrae.fr/irbas/

Bacteria

“Everything is everywhere, the environment selects.” A statement relative to the size of the observer, and the size of the observed, but can be used in this case (concerning bacteria) and even the case of fungi and diatoms. Bacteria are ubiquitous, and one of the quickest biota to colonize the environment, especially after a big change such as drying or rewetting, their presence or absence, and the composition of their community can give us a lot of information about the environment (e.g. CSR strategies). Dry and wet phase of Drying River Networks (DRNs) usually exchange rapidly, and it is important to note that habitat (e.g. type of sediment, presence of leaf litter as a form of moist refuge for microbes) and the severity, longevity and dynamics of drying events (e.g. flash floods present, long dry periods) greatly influence local microbial communities (Mora-Gomez et al. 2020; Gionchetta et al. 2020). Environmental conditions and mentioned dynamic influence and determine local habitat biodiversity, community, and as a result, ecosystem functioning (Baldwin and Mitchell 2000; Datry et al. 2017; Gionchetta et al. 2020). The trait approach in bacterial communities can give perspective in many different angles. It can describe their ability to survive disturbances with traits such as entering dormancy (Jones and Lennon 2010). How their function such as primary production and organic matter degradation is improved or impaired (Mora-Gomez et al. 2020). Also, what is the side effect of their presence and how it influences the environment around them (Romani et al. 2013).

Literature coverage of for traits of bacteria can be somewhat confusing. Great number of descriptions of bacterial traits exists, but they is not directly listed and described as traits, rather as functions. When concerning the trait and functional approach to bacteria and their resistance and resilience to drying, almost all focus is turned to agriculture and soil ecology, while none so to freshwater ecology. It is possible to extrapolate data from existing literature (also using tools as CSR strategies to classify bacterial niches), but as interest in the direction of bacterial resistance to drying of freshwater bodies is low, so is the amount of literature.

Bacteria database:

BactoTraits database is a user friendly bacterial trait database. It contains information on 19455 bacterial strains and has a purpose of evaluation of natural and man-made influences on bacterial communities. It contains information on the following bacterial traits: oxygen preference, size and shape of bacteria, motility, optimum and range of pH and temperature, genome GC percent and trophic type (Cébron et al. 2021).

https://ordar.otelo.univ-lorraine.fr/record?id=10.24396/ORDAR-53

List of important traits for coping with drying:

Resistance traits:

- **Osmolyte production**

A physiological response to drying resulting in the production of osmolytes, substances with a purpose of reducing the water potential and maintaining cell hydration. This trait should be fuzzy coded, as its presence depends on the bacterial taxonomic group can be present and in different measures and forms. (Gionchetta et al. 2019)

Physiological, categorical – e.g., binary (yes or no), expert opinion/high coverage, high chance of survival

- **EPS production**

Extracellular polymers or Extracellular polymer substances (EPS) are secreted by some microorganisms. Fundamentally they provide protection to the organisms in array of ways hence even ensuring the survival of assemblages under stress events. EPS production puts strain on the organisms producing them and it may also make them less competitive (for resources) compared to non-producing (Jayathilake et al. 2017). It is nevertheless a physiological, and shared trait by many microorganisms and also to some macroinvertebrates and fish. A direct or indirect product of metabolism or life history. Results as a protective layer from outer (negative) influence. In case of drying, it protects the organism for a limited period of time (two to three weeks) and can be used as an example for the importance of periodic rainfall which revitalizes the organism. While full rewetting is not needed for the population survival (Allison and Goulden 2017; Gionchetta et al. 2019).

Physiological, categorical – e.g., binary (yes or no), expert opinion/high coverage, low chance of survival

- **Cell wall structure**

Gram-positive or Gram-negative bacteria got their name from the method of dyeing devised by Hans Christian Gram and the two generally different results showed differences in morphology and physiology. Gram positive bacteria do not have outer membrane, their lipopolysaccharide (LPS) content is almost negligible, but they create a thick interlinked peptidoglycan wall (thick cell walls), characteristic opposite than in gram negative bacteria (University of Maryland 2000). The resulting peptidoglycan wall is high cost in terms of energy, carbon and nitrogen input, but provides protection against drying events. As such it can be used as an indicating trait if the habitat is undergoing periodical drying events (Schimel et al. 2007).

Physiological, categorical – e.g., binary (G+ and G-), expert opinion/high coverage, medium chance of survival

- **Alteration of membrane composition or LPS modification**

Gram-negative bacteria have LPS lipopolysaccharide and phospholipids associated with the cell membrane. It is an important property and provides the a barrier function. Membrane composition is a mechanism that either helps protecting susceptible cellular components from damage, or that sequester water in an attempt to avoid dehydration. It helps to stabilize membranes during drying, and the accumulation of compatible solutes which can protect cytoplasmic and membrane constituents (Schimel et al. 2007).

Physiological, categorical – e.g., binary (yes or no), low coverage, low chance of survival

Resilience traits:

- **Capsule production**

Capsules (generally polysaccharide in nature) are formations on the microorganism's (bacterial) surfaces. It may be the first point of contact (and communication/interaction) with new organism and environment. Capsular synthesis that helps form “sponges” to retain water in cell envelopes. Provides protection from long-term drying event (two or more years). It can be used as a trait of high importance that describes the ensured survival of the population in case of drying event (Malik et al. 2020).

Physiological, categorical – e.g., binary (yes or no), expert opinion/high coverage, high chance of survival

- **Ability to enter dormancy**

Entering a dormant state is a characteristic present in most major taxonomic groups. To enter a dormant state means to lower the organism activity, which lowers metabolic activity and hence the demand for food and energy. It is a mechanism that is used to survive harsh conditions such as freezing, drying, or any other extreme conditions. Bacteria and fungi have that ability and in doing so they become a member of the seed bank. Used as a strategy to survive unfavorable conditions such as drying of the riverbed (Jones and Lennon 2010; Gionchetta et al. 2018; Polozsányi et al. 2021).

Physiological, categorical – e.g., binary (yes or no), expert opinion/high coverage, medium chance of survival

- **Ability to burrow / survive in sediment**

Interaction of sediment grain size, organism size and mobility. Tendency of an organism to seek refuge in sediment which retains moisture for a longer period which ensures their survival of the drying event. Drying sediment, especially slow drying sediment provides a level of protection in the form of postponing the drying of the microorganism. Extracellular enzyme activity shows favorable conditions of the slow drying sediment for the microorganism which continued its metabolic activities eight weeks after the drying event (Shade et al. 2012; Pohlon et al. 2013).

Behavioral, categorical – e.g., binary (yes or no), high coverage, medium chance of survival

Fungi

Similar as bacteria, fungi can fall under the same concepts and rules and share some of the traits. In soils and riverbeds, bacteria and fungi share their habitat and often live in mutualism or competition (Bastida et al. 2016). Fungi have a very important, possibly the most important role in nutrient cycling. Their ability to dissolve organic matter, colonize and survive in leaf litter and detritus, and the fact that they make 55 – 89% of microbial biomass on average, adds to the former statement (Treseder and Lennon 2015). Fungi have been proven to endure pulse and pressure disturbances better than their other microbial counterparts. While some parts of fungal community may be more vulnerable to such events, its utilization of local vegetation, colonization of sediments and detritus makes it most resilient (Foulquier et al. 2015; De Vries et al. 2018; Bardgett and Caruso 2020).

Determining the approach to this group has proven most difficult. The reason being a small amount of research. Fungi are a biota of a cryptic lifestyle that needs to be molecularly identified. Even though molecular methods have recently became much cheaper and more accessible knowledge about functional traits of fungi is vague and utilizing of environmental data remains a challenge (Põlme 2020). Since fungi are the least researched group of the five mentioned, it is also difficult to establish contact with relevant experts.

Fungi with micellar growth and/or motile spores are highly resistant and resilient to drying. That means that in if a rewetting event occurs after a drought long enough for freshwater habitats to turn into land habitats, the populations of fungi that have the listed traits would be almost instantly recovered.

Fungi databases:

FUNGuild has been recommended by experts and will be used if there will be gaps to fill. It is a a Python-based database that can be used to pair operational taxonomical units by ecological guild. (Nguyen et al. 2016).

http://www.funguild.org/

GlobalFungi is the main database when gathering data on fungi. The GlobalFungi database contains over 600 million observations of fungal sequences over more than 17 000 samples with geographical locations and additional metadata. It is the most comprehensive atlas of global fungal distribution, and it is designed so that the third-party data addition is possible. It contains information on sample type, pH, geography, biome, and metadata of the sample (Větrovský et al. 2020).

https://globalfungi.com/

FunFun aka **fungaltraits** database was created by cooperation of 23 fungal and plant ecologists, systematists and bioinformaticians. It was built to utilize trait based approaches can provide new insights in fungal functional ecology (Flores-Moreno et al. 2019).

https://github.com/traitecoevo/fungaltraits

List of important traits for coping with drying:

Resistance traits:

- **Melanized cell walls**

Melanin is a condensed, randomly arrayed, aromatic pigment that is located in the cell wall or extracellular matrix of fungi. It broadly protects fungi from an array of environmental stresses, including extreme heat and cold, drought, UV radiation, high salinity, heavy metals, and anthropogenic pollutants (Treseder and Lennon 2015).

Physiological, categorical – e.g., binary (yes or no), expert opinion/high coverage, medium chance of survival

- **Beta 1,3-Glucan production**

Glucans are glucose polysaccharides which can be abundantly distributed in the cell walls of fungi. They are macromolecules that can have different configurations; α or β configuration, and different degrees of polymerization. It forms cross-linkages with chitin and other components: improve the strength and integrity of the cell wall under a range of stress such as providing structure and defense against invaders, protection against dehydration and they can act as an energy reserve during critical periods of their development (Dalonso et al. 2015; Treseder and Lennon 2015).

Physiological, categorical e.g., binary (yes or no), expert opinion/high coverage, medium chance of survival

- **Trehalose production**

Trehalose is a sugar in which the two glucose units are linked. This disaccharide is present in a wide variety of organisms, such as bacteria, yeast, fungi, insects, invertebrates, lower and higher plants, where it may serve as a source of energy and carbon. It has been shown that trehalose can protect proteins and cellular membranes from inactivation or denaturation caused by a variety of stress conditions, including desiccation, dehydration, heat, cold, and oxidation (Elbein et al. 2003). It is a solute that is thought to substitute for water molecules in cell membranes, protecting them from desiccation and freezing damage. Also acts as a compatible osmolyte as well as protection from heat shock (Treseder and Lennon 2015).

Physiological, categorical – e.g., binary (yes or no), expert opinion/high coverage, medium chance of survival

- **Osmolyte production**

A physiological response to drying resulting in the production of osmolytes, substances with a purpose of reducing the water potential and maintaining cell hydration. This trait should be fuzzy coded, as its presence depends on the bacterial taxonomic group can be present and in different measures and forms (Gionchetta et al. 2019).

Physiological, categorical – e.g., binary (yes or no), expert opinion/high coverage, low chance of survival

- **EPS production**

Extracellular polymers or extracellular polymer substances (EPS) are secreted by some microorganisms. Fundamentally they provide protection to the organisms in array of ways hence even ensuring the survival of assemblages under stress events. EPS production puts strain on the organisms producing them and it may also make them less competitive (for resources) compared to non-producing. It is nevertheless a physiological, and shared trait by many microorganisms and a similar characteristic to some invertebrates and fish. A direct or indirect product of metabolism or life history. Serves, or better said results as a protective layer from outer (negative) influence. In case of drying riverbed, it protects the organism for a limited time period (two to three weeks) and can be used as an example for the importance of periodic rainfall which revitalizes the organism. While full rewetting isn't needed for population survival (Allison and Goulden 2017; Gionchetta et al. 2019).

Physiological, categorical – e.g. binary (yes or no), expert opinion/high coverage, low chance of survival

Resilience traits:

- **Mycelial growth**

Mycelia is a vegetative body of fungi. It is similar to a root like structure that consists of high branching. Mycelial growth can be described as ubiquitous and is very important for organic matter decomposition in soil and aquatic ecosystems. Its capability to spread and access throughout the ground provides it with high amount of nutrients, water and shelter and is one of the most important if not the most important fungal trait for drying survival. While unsheltered mycelium may be vulnerable to conditions such as drying and/or freezing, it provides resources as well as survival of its more protected parts, which is responsible for quick recolonization after rewetting (Gionchetta et al. 2019; Schimel et al. 2007; De Boer et al. 2005).

Physiological, categorical – e.g., binary (yes or no), expert opinion/high coverage, high chance of survival

- **Motile spores**

Otherwise called fungal zoospores are capable of flagellar movement in water and ameboid movement on open surfaces. Fungal taxa that create such spores have a much higher range of dispersal and if they are in water with unfavorable conditions, they can encyst themselves or attach to an appropriate substrate (Gleason and Lilje 2009). Mentioned in Gionchetta et al. 2019 and emphasized by Dr. Petr Baldrian and Dr. Anna Maria Romaní in an interview as a trait that almost ensures the survival of the fungi.

Physiological, categorical – e.g., binary (yes or no), expert opinion/high coverage, high chance of survival

- **Forming endophytes**

Endophyte forming fungi establish communities in different hosts. They colonize intercellular and intracellular tissues of their hosts, plants of various life histories, which provide shelter and refuge during extreme conditions (Beena et al. 2021). Survival in roots exposed to water, leaf litter on stream banks and riparian tree canopies. Used to survive in arid areas and transfer nutrients between plants and nearby soil (De Boer et al. 2005; Ghate and Sridhar 2015; She et al. 2018).

Physiological, categorical – e.g., binary (yes or no), low coverage, medium chance of survival

- **Spore dispersal ability regarding sediment grain and spore size**

Different species of fungi have different interaction with the different types of sediment. Sediment wise it mostly relates to grain size and porosity, while spores that are smallest in size have an advantage of dispersing in the hyporheic. Other factor contributing to spore dispersal regarding their size is higher chances of attachment to surfaces by bigger spores which inhibits their abilities to travel deeper in sediment and thus be more protected from drying (Tesmer and Schnittler 2007; Cornut et al. 2014).

Reproductive, fuzzy – e.g., (low, medium, or high dispersal), low coverage, medium chance of survival

- **Spore shape**

Difference in fungi spore shapes influences their ability to be transported in sediment and thus changes the amount and depth of fungi spores present in the hyporheic. No matter the sediment size, dispersal ability of filiform/sigmoid spores was always significantly higher than that of the three other species with compact and branched/tetraradiate spores. Stronger attachment to surfaces caused by mucilage at the tip of the spore arms can have a negative effect for dispersal (Cornut et al. 2014).

Reproductive, categorical (globose, cylindrical, allantoid and elongated), low coverage, medium chance of survival

- **Ability to enter dormancy**

Entering a dormant state is a characteristic present in most major taxonomic groups. To enter a dormant state means to lower the organism activity, which lowers metabolic activity and hence the demand for food and energy. It is a mechanism that is used to survive harsh conditions such as freezing, drying on any other extreme conditions. Bacteria and fungi have that ability and in doing so they become a member of the seed bank. Used as a strategy to survive unfavorable conditions such as drying of the riverbed (Jones and Lennon 2010; Gionchetta et al. 2018; Polozsányi et al. 2021) .

Physiological, categorical – e.g. binary (yes or no), expert opinion/high coverage, medium chance of survival

Diatoms

Taxonomically complex and diverse communities of diatoms are sensitive to many environmental variables, including light, moisture conditions, temperature, current velocity, salinity, pH, oxygen, inorganic nutrients, organic carbon, and organic nitrogen (Van Dam et al. 1994). As such, freshwater diatoms have been used in aquatic environmental assessment for more than a hundred years, and new indices are still being developed (Kahlert et al. 2021). While the environmental effect on functionality of this biota is above average covered, the lack of information is still noted (Novais et al. 2020). Drying greatly affect the community structure of diatoms, as it is showed that the functional richness was significantly lower in intermittent than in permanent streams (Novais et al. 2020). A trait-based approach could be used in the coming future because traits are the manifestation of diatom functioning in each environment, and traits could be used to more accurately describe habitats with unknown diatom communities (Kahlert et al. 2021).

Diatom databases:

Freshwater benthic diatoms is a database created by Rimet and Bouchez 2012 containing information on Life-forms, cell-sizes and ecological guilds of diatoms in European rivers.

https://entrepot.recherche.data.gouv.fr/dataset.xhtml?persistentId=doi:10.15454/XLQ40G

Phytoplankton of temperate lakes is a database containing physiological and morphological trait information (Rimet and Duart 2018).

https://zenodo.org/record/1164834#.ZEFe7HZBxhE

Phytoplankton morpho-functional trait dataset from French water-bodies was also used to code some of the diatom traits (Derot et al. 2020).

https://entrepot.recherche.data.gouv.fr/dataset.xhtml?persistentId=doi:10.15454/GJGIAH

List of important traits for coping with drying:

Resistance traits:

- **Biofilm production of protective extracellular matter**

Biofilm can be defined as a layer of mucilage covering a usually solid surface (sometimes it can be mud) containing a community of microorganisms, often, a more than one biota inhabits the biofilm. Diatom biofilm consists of diatom community and EPS (extracellular polysaccharide matrix) in which the organisms are embedded. EPS is composed of about 95% saccharides and stabilized by lipoproteins. Diatoms create two different EPS, liquid culture EPS and sediment EPS that differ in their composition, but both provide protection from drying events (Stal and de Brouwer 2003; Koedooder et al. 2019). After a short water flux, dry biofilm rewets and reveals revitalized diatoms which shows their capacity for survival in said form (Novais et al. 2020).

Morphological, categorical – e.g. binary (yes or no), common knowledge, medium chance of survival

- **Colonial/non colonial/form of colony**

Diatoms can appear as a singular cell or in the form of colonies can take the shape of ribbons, fans, zigzags, or stars, and both life forms (singular or colonial) can have its advantages and disadvantages in drying survival (Nakov et al. 2015). Colonies promote the adhesion to the substrate by creating a moist microhabitat useful to withstand the drying period (Rimet and Bouchez 2012; Sancho et al. 2020).

Life form, categorical – (colonial, single cell, ribbon, arbuscular), common knowledge, low chance of survival

- **Non colonial**

Free moving individual cells may be able to disperse easily (Rimet and Bouchez 2012; Lange et al. 2015; Sancho et al. 2020).

Life form, categorical – e.g., binary (colonial and single cell), common knowledge, low chance of survival

- **Ribbon (colonial) forming diatoms**

Promotes the adhesion to the substrate by creating a moist microhabitat useful to withstand the drying period (Rimet and Bouchez 2012; Sancho et al. 2020).

Life form, categorical – e.g., binary (yes or no), common knowledge, low chance of survival

- **Arbuscular**

Arbuscular colonies are formed by cells secreting mucilaginous stalks and forming ramifications diverging from each cell. The stalks contain extracellular enzymes that give them the ability to consume macromolecules and act as a nutrient pump, which makes them more resilient to pressures and disturbances (Rimet and Bouchez 2012; Marcel et al. 2017).

Life form, categorical – e.g. binary (yes or no), common knowledge, low chance of survival

- **Cell size**

Large diatoms tend to be epipelic, at the interface of sediments and water, therefore having more potential abilities to survive in dry sediments (Lange et al. 2015; Sancho et al. 2020). Taxa with a fast-growing rate (smaller in size), may be competitive in recolonizing (Sancho et al. 2020).

Morphological, continuous (0 - ∞), medium coverage, low chance of survival

- **Adnate**

The adhesion to the substrate by their valve face or girdle view, promotes a moist microhabitat in which they may withstand the drying period, and they are less susceptible to turbulences (Rimet and Bouchez 2012; Sancho et al. 2020).

Life form, categorical – e.g. binary (yes or no), common knowledge, low chance of survival

- **Pedunculate**

Pedunculate cells produce a mucilaginous peduncule by secreting it from their apex. The peduncule, depending on it’s length can be defined as a “pad” (short peduncule) and a stalk (long peduncule) (Marcel et al. 2017). The production of mucilage on a pole that sticks to substrate may be useful to stay hydrated (Rimet and Bouchez 2012; Sancho et al. 2020).

Life form, categorical – e.g. binary (yes or no), common knowledge, low chance of survival

- **Planktonic guild**

Taxa included in this guild are adapted to lentic environments, having morphological adaptations that enable them resisting to sedimentation (Sancho et al. 2020; Passy 2007). Planktonic diatoms are also well adapted to regimes of intermittent light and nutrient exposure, and their planktonic way of life highly increases their distribution (Malviya et al. 2016; O’Brien et al. 2022).

Behavioral, categorical – e.g. binary (yes or no), medium coverage, low chance of survival

- **Moisture tolerance**

Terrestrial diatoms have an ability to survive in soils with over 50% of water content, as such, low moisture tolerance can be an important trait for surviving drying events if located in moist sediment. (van Dam et al. 1994; Souffreau et al. 2010; Sancho et al. 2020)

Physiological, categorical (never, or only very rarely, occurring outside water bodies), low coverage, low chance of survival

- **Nitrogen fixation**

Nitrogen fixation is one of the key traits that showed the strongest relationship with environmental stressors. N-fixing algae access an additional nitrogen source (advantage under nutrient-limiting conditions) (Lange et al. 2015). Another source of nitrogen can be endosymbiotic N-fixing cyanobacteria which enables nutrient reduction in ponds (van Dam et al. 1994). Recommended by experts as a form to survive in extreme conditions.

Physiological, categorical (nitrogen-autotrophic taxa. Tolerating very small concentrations; nitrogen-autotrophic taxa, tolerating elevated concentrations; facultatively nitrogen-heterotrophic taxa, needing periodically elevated concentrations; obligately nitrogen-heterotrophic taxa, needing continuously elevated concentrations), high coverage, low chance of survival

- **Areolae morphology**

Reduced number of areolae or they are occluded with a siliceous lamina. Both characteristics minimize loss of water or retain cellular moisture (Lowe et al. 1992).

Morphological, fuzzy coded (low number – high survival, medium number, high number), low coverage, low chance of survival

- **Aerophile**

Taxa often present in intermittent streams and can be used as an indicator of dry phases. Mainly occurring in water bodies, sometimes on wet places, mainly occurring in water bodies, also rather regularly on wet and moist places, mainly occurring on wet and moist or temporarily dry places, nearly exclusively occurring outside water bodies (van Dam et al. 1994; B-Béres et al. 2022).

Physiological, categorical – e.g., binary (yes – no), common knowledge, medium chance of survival

Resilience traits:

- **Ability to burrow / survive in sediment**

By providing organic matter, presence of diatoms in sediments can improve the state of the microbial communities (Jewson et al. 2007). Some diatoms have the ability of long-term survival in the hyporheic which provides them shelter from hash conditions (Lewis et al. 1999). Dry sediments, organic matter and moist leaves can maintain a certain humidity for them to endure the drying periods facilitating the recovery (Sancho et al. 2020).

Behavioral, categorical – e.g., binary (yes and no), common knowledge, low chance of survival

- **Shape**

Diatoms vary in shape which influences their movement speed as well as the ability to access nutrition and shelter (in sediment). Elongated shapes avoid being buried by sedimentation (Edgar 1982). And hydrodynamic outline gives diatoms the ability to escape unfavorable conditions faster.

Morphological, categorical (elliptic cylinder (noted ellcyl), rhomboid prism (noted rhp), box (noted box), sphere (noted sphe), tube (tub), low coverage, low chance of survival

- **Oxygen requirements**

May be able to endure the anoxic conditions in remnant pools with accumulated organic matter (Sancho et al. 2020). Some diatoms as well as many other organisms when exposed to hypoxic conditions have the capability of changing some of their metabolic pathways (e.g., transition from mitochondrial respiration to fermentation) to better endure unfavorable conditions that might occur during water scarcity (Zhao et al. 2022).

Physiological, categorical – (0 - unknown; 1 - very high > 8 mg/l; 2 - high 7-8 mg/l; 3 - moderate 7-4 mg/l; 4 - low 4 mg/l; 5 - very low < 4 mg/l), high coverage, medium chance of survival.

- **Mobile**

Even though the taxa for this guild is characteristic for perennial streams, their mobility gives them the capability to avoid drying. They can move on the stone surface, remaining in contact with the water, as the upper part of the river dries faster. May be able to select their habitat and locally migrate to parts with moisture under the stone (Sancho et al. 2020 as cited from Passy 2007; Rimet and Bouchez 2012; B-Béres et al. 2022).

Behavioral, categorical – e.g., binary (yes and no), high coverage, low chance of survival

- **Pioneering**

Able to endure harsh drying conditions, described as part of the low profile guild with a very high capacity for recolonization, these species are the first to colonize the disrupted environment (Sancho et al. 2020 as cited from Passy 2007; Peszek et al. 2021).

Life strategy, categorical – e.g., binary (yes and no), medium coverage, medium chance of survival

- **Guild profile: Low/High**

Low profile guild has a high capacity for reproduction and dispersal which increases disturbance resistance.

High profile guild is sensitive to turbulence, but it benefits from nutrient enrichment as opposed to low profile guild. It includes large or colonial species (Sancho et al. 2020).

Low and high profile guilds can be used as an indicator for disturbances as it is a trade off and their presence indicates different sets of pressures and stresses. Low profile guild has a higher presence during the warm periods of the year which is an indication of adaptation to water scarcity (Stenger-Kovács 2013).

Life strategy, categorical – e.g., binary (low – high), high coverage, low chance of survival

- **Main reproductive feature (strategy)**

Fission generally produces smaller propagules than fragmentation. This may be advantageous for dispersal and recolonization after disturbance (Lange et al. 2015). Formation of thick-walled, dormant spores (akinetes, oospores, zygospores) enables cells to endure unfavorable conditions (Lange et al. 2015).

Reproductive, categorical (Sexual, Asexual), high coverage, low chance of survival

- **Resting spores**

Resting spores are a life history trait of diatoms and their purpose is harsh conditions survival. They are characterized by greatly slowed metabolism and growth, and a thick silica frustule that gives them protection from darkness which enables the diatom to survive in sediment and under ice (Fryxell et al. 1981). It also gives them the ability to survive periods of stress up to several millennia (Sanyal et al. 2021).

Life strategy, categorical – e.g., binary (yes – no), common knowledge, high chance of survival

- **Resting cells**

Resting cells (also called resting stage cells and vegetative cells) are dormant benthic cells produced by asexual reproduction for centric diatoms and sexual reproduction by dinoflagellates. Although resting spores and resting cells hold the similar purpose in life history of diatoms they differ in morphological/physiological features. While resting or vegetative cell does not differ from the dormant cell in morphology, rather only in physiology, resting spore is characterized by a thick cell wall. They have a high capability of surviving adverse conditions for a long time (Sicko-Goad et al. 1989).

Physiological, categorical – (akinete, heterocyst, cyst), common knowledge, high chance of survival

- **Taxa influenced by mass effect**

Mass effect is the ability of a species to inhabit an unsuitable habitat patch or a sink as a result of a high dispersal rates from suitable habitat patches or sources. Species capable of mass effect have a high dispersal rate and as such have the ability to rapidly colonize and recolonize habitats after rewetting (Leboucher et al. 2021).

Behavioral, eco physiological, categorical – e.g., binary (yes – no), common knowledge, medium chance of survival

Aquatic Macroinvertebrates

Because of their taxonomical and functional diversity, as well as size that makes them easily accessible and identifiable, aquatic macroinvertebrates community structure is one of the most widely used indicator for ecosystem health. Trough time, many different approaches and indexes are being developed to gain a better insight in aquatic invertebrates and trough that, the environment. Species traits are the characteristics that can be used to better understand an organisms' relationship to the surrounding environment, including growth, feeding habits, drying events survival, and dispersal via the changes in community functioning (EPA 2012). In comparison to the presence/absence approach, functional trait approach can better follow changes in functional community characteristics and will greatly improve our ability to predict the impact of environmental change on ecosystems (Dezerald et al. 2015).

Trait approach can be versatile and widely applicable. It can be used from many different starting points to describe and better understand the connections between inhabitants of the ecosystem, their function, environmental influence, and in the end, consequence. One example of trait approach is the DISPERSE database which has been established to better understand and utilize the function of aquatic macroinvertebrate dispersal, which is an essential process in population and community dynamics. Through the movement of individuals and species, dispersal strongly influences metapopulation and metacommunity dynamics. A better understanding of dispersal processes can inform biodiversity management practices (Sarremejane et al. 2020).

Aquatic macroinvertebrate databases:

DISPERSE database is only referential (orientational) and subject to permission protocol. It will be used as a model for current database creation, as well as a source of information that can help in better understanding the drying resistance and resilience traits of aquatic macroinvertebrates (Sarremejane et al. 2020).

https://www6.inrae.fr/irbas/News/DISPERSE-db

EPA freshwater biological traits database is a trait database on North American freshwater macroinvertebrates (EPA 2012).

https://www.epa.gov/risk/freshwater-biological-traits-database-traits

Species Traits Analysis by (Usseglio-Polatera and Bis 2004) was used to find and code some of the traits.

http://www.eu-star.at/pdf/Deliverable_N2.pdf

List of important traits for coping with drying:

Resistance traits:

- **Oxygen preference**

Deficit of dissolved oxygen levels in water is often corelating with water scarcity and both are significant stressors of Mediterranean freshwater systems and communities present in them. It can lead to changes in the biological traits of invertebrates (Calapez et al. 2018). High concentration of dissolving organic matter in small water bodies and sediment can lead to low concentrations of oxygen which influences survival, growth, feeding and reproduction primarily. Therefore, organisms that possess oxygen-binding metalloproteins have a higher chance hypoxia and therefore drying survival (Galić et al. 2019).

Physiological, fuzzy (no strong preference, low, moderate, moderate-high, high), high coverage, low chance of survival

- **Physicochemical resistance**

Physicochemical stability correlates with species abundance of aquatic ecosystems. During drying events, isolated pools or wet sediment can provide refuge for aquatic macroinvertebrates. Water in those refuges often suffers extreme conditions and organisms with high physicochemical tolerance have higher chance of survival (Death and Winterbourn 1995; Brown et al. 2006).

Physiological, fuzzy (tolerant (tol), moderately tolerant (mtol), moderately sensitive (msen), sensitive (sen), highly sensitive (hsen)), medium coverage, medium chance of survival

- **Diapause**

Genetically programmed response influenced by physical conditions. A delay in development or suspended development in any phase of an invertebrate (egg, larva, pupa, adult) that can be utilized in survival of unfavorable environmental conditions (Panov et al. 2004; Alekseev et al. 2007; Alekseev 2010).

Physiological, categorical e.g., binary (yes or no), common knowledge, medium chance of survival

- **Respiration**

During a drying event, aerial respiration improves survival over other types of breathing (LeRoy Poff et al. 2006; Aspin et al. 2019).

Physiological, categorical (tegument, gills, plastron, spiracle (aerial)) common knowledge, medium chance of survival

Resilience traits:

- **Resting eggs**

Several different groups have a development pause during an embryonic stage such as an egg or a spore. The purpose of the mentioned pause is often connected with the endurance and survival of harsh conditions such as freezing, drying, lack of resources and energy. This life history trait can protect an organism for tens or hundreds of years (even thousands when concerning microbes) (Clark et al. 2012). It is also a resistant life stage in many members of freshwater macroinvertebrate community. Desiccation resistant eggs (Kefford et al. 2020). Resting eggs or desiccation resistant eggs can provide a great level of protection and chance of survival in dry waterbodies sediments with certain level of interstitial moisture is still present (Stubbington et al. 2016).

Reproductive, categorical – e.g., binary (yes or no), high coverage, low chance of survival

- **Burrowing**

Burrowing in sediment can greatly increase the chances of drying survival of freshwater macroinvertebrates. Some groups (e.g. isopods) actively burrow in sediment, while others can keep refuge in existing shelters by avoiding higher temperatures during a drying event. After the drying of a water body, sediments dry much slower and as such can provide shelter for some species that usually dwell on its surface (Strachan et al. 2014).

Behavioral, categorical e.g., binary (yes or no), medium coverage, medium chance of survival

- **Armor**

During drying easier to find refuge and cover in hyporheic zone, shallow depressions, and beneath woody debris. Easier to avoid predation (Rader 1996; LeRoy Poff et al. 2006).

Morphological, categorical (All sclerotized, Hard shelled, Partly sclerotized, Soft), medium coverage, low chance of survival

- **Encysting (resisting in cocoons or housings)**

Certain invertebrates (e.g., Ostracoda, Baetidae, Simuliidae, Ceratopogonidae, Chironomidae, and Plecoptera) can encyst or aestivate in the dry riverbed which gives them high probability of surviving the drying event. An encysted egg or embryo contains an accumulation and enrichment of specific compounds that can support long-term dormancy (Rozema et al. 2019).

Physiological, categorical e.g., binary (yes or no), common knowledge, medium chance of survival

- **Short generation time**

One of the traits associated with the resilience of the whole population. If present in a species, its population has the ability to hastily recolonize rewetted location (Dolédec et al. 2006). It can be optimal and suboptimal regarding generational time of macroinvertebrates and habitat time without disturbances (Verberk et al. 2008).

Reproductive, numerical (< 1 year, > 1 year), common knowledge, medium chance of survival

- **Asexual reproduction**

Provides the same population function as the short generation time. Trait associated with the population resilience. If present in a species, a population is able to hastily recolonize rewetted location (Dolédec et al. 2006)

Reproductive, categorical e.g., binary (yes or no), common knowledge, medium chance of survival

- **Voltinism**

Voltinism can greatly affect range of a species. Shorter generation time allows species to react quicker to changing conditions in extreme environments and survive them (LeRoy Poff et al. 2006; Maran and Pelini 2016).

Reproductive, categorical (<1, 1, >1), common knowledge, medium chance of survival

- **Development**

Faster development of organisms leads to greater ability to avoid drying events (LeRoy Poff et al. 2006).

Physiological, categorical (fast seasonal, slow seasonal, nonseasonal), common knowledge, medium chance of survival

- **Synchronization of emergence**

Synchronized emergence contributes to greater survival of extreme conditions (Semlitsch et al. 1988; LeRoy Poff et al. 2006).

Behavioral, categorical binary (poorly synchronized, well synchronized) common knowledge, medium chance of survival

- **Adult lifespan**

Longer adult life span can have a positive effect on drying survival. Species with longer adult life spans may be better able to survive prolonged droughts, as they have more time to reproduce and produce offspring that are adapted to these conditions (LeRoy Poff et al. 2006; Verberk et al. 2008).

Physiological, categorical (< 1 week, < 1 month, 1month - 1 year, > 1 year), common knowledge, medium chance of survival

- **Adult ability to exit**

Ability to exit or emerge from the body of water greatly improves the dispersal range of macroinvertebrates as well as improve their chances of drying survival in the form of drying event avoidance (LeRoy Poff et al. 2006).

Behavioral, categorical (absent, present), common knowledge, high chance of survival

- **Female dispersal**

Female dispersal plays an important role in drying event survival as it allows females to find suitable habitats when their dries up (LeRoy Poff et al. 2006).

Behavioral, categorical (low (<1 km flight before laying eggs), high (>1 km flight before laying eggs)), common knowledge, medium chance of survival

- **Adult dispersal ability**

Similar to female dispersal, adult flying strength improves covered distance which in turn improves finding a suitable habitat for drying survival (LeRoy Poff et al. 2006).

Behavioral, categorical (1 km or less, 10 km or less, 100 km or less), common knowledge, medium chance of survival

- **Occurrence in drift**

Improves mobility and accessibility to suitable habitats during drying events (LeRoy Poff et al. 2006).

Behavioral, categorical (rare (catastrophic only), common (typically observed), abundant (dominant in drift samples)), common knowledge, medium chance of survival

- **Maximum crawling rate**

Improves mobility and accessibility to suitable habitats and refuge during drying events (LeRoy Poff et al. 2006).

Behavioral, categorical (very low (<10 cm/h), low (<100 cm/h), high (>100 cm/h), common knowledge, medium chance of survival

- **Swimming ability**

Improves mobility and accessibility to suitable habitats during drying events (LeRoy Poff et al. 2006).

Behavioral, categorical (none, weak, strong) common knowledge, medium chance of survival

- **Size at maturity**

During drying events, organisms with lower metabolic rates have a higher chances of survival which makes bigger organisms favorable for drying survival. (LeRoy Poff et al. 2006; Aspin et al. 2019)

Opposite to that small size has been widely described as a biological trait useful for survival of species. Most of the assemblages of hyporheic zones of sandy stream is composed of meiofauna (e.g. body size < 1000µm) (Malard et al. 2002). Although it ensures easier avoidance of predators, especially during water scarcity, such species have a higher chance of finding refuge, shelter, and can burrow in smaller spaces during heightened environmental pressures (Rader 1996; Usseglio-Polatera et al. 2000; LeRoy Poff et al. 2006)

Physiological, categorical (< 0.25 cm, > 0.25 - 0.5 cm, > 0.5 - 1 cm, > 1 - 2 cm, > 2 - 4 cm, > 4 - 8 cm), common knowledge, medium chance of survival

- **Lifelong fecundity**

Lifelong fecundity is the number of eggs a female produces. More production means more chances to avoid drying events. (Sarremejane et al. 2020)

Physiological, numerical (< 100; ≥ 100–1000; ≥ 1000–3000; ≥ 3000), common knowledge, medium chance of survival

Fish

Drying events can greatly influence and decline abundance, distribution and altogether, biodiversity of fish (Crook et al. 2010). To use as an example for Europe, Mediterranean river fish assemblages are among the most poorly known. These rivers are subject to a characteristic climatic regime, seasonal droughts and inflows which are getting more unpredictable and are highly variable between years. Drying can provoke major habitat and connectivity losses and consequent large declines in the fish populations (Moran-Lopez et al. 2006). Increased need for water use, such as agricultural irrigation can be an additional pressure to already disturbed freshwater environments in arid climates (Skoulikidis et al. 2011). Although we take the approach of drying resistance and resilience traits to fish, their survival may much more depend on habitat geology, structure and potential to seek refuge as there is no fish species in Europe capable to survive a complete dehydration of the riverbed (Hershkovitz and Gasith 2013). Here we focus on physiological but mostly behavioral fish traits. To gain insight in their composition as an indicator of habitat state is possible, but it is important to note that species of high abundance and distribution may have difference in level of traits among its' populations (Crook et al. 2010).

The approach of traits is not so common. Fish are not so often regarded as a community, rather as a species or a population. Fish are highly covered by literature.

Fish databases:

The TOFF (i.e. Traits OF Fish) database contains information on behavioral, morphological, phenological, and physiological traits of fish (Lecoq et al. 2019). These categories are divided in subcategories, and some of the traits can be used to determen the ability to endure and survive a drying event and are included in this text.

https://toff-project.univ-lorraine.fr/

FishBase is a database containing spatial, environmental and trait information on 35000 species of fish (Froese and Pauly 2022).

https://www.fishbase.se/search.php

List of important traits for coping with drying:

Resistance traits:

- **Physicochemical tolerance**

During drying events, fish can survive in refugia or aestivation (not present in European freshwater fish). Such scarce amounts of water more often than not put high amount of physicochemical pressure on present organisms. Ability to withstand high temperatures, low dissolved oxygen, high conductivity, changes in pH and low nutrient content provide higher chance of drying event survival (Crook et al. 2010; Magoulick and Kobza 2003).

Physiological, fuzzy (level of distinction i.e., boundaries to be decided), complete coverage, low chance of survival

- **Thermotolerance**

During drying events and water scarcity, species of fish with tolerance to higher temperatures have a higher chance of drying survival (Griswold et al. 1982).

Physiological, quantifiable, continuous (the level of tolerance a species can endure without stress), complete coverage, medium chance of survival

- **Hypoxia tolerance**

Some fish such as cyprinids use lactic acid fermentation, also known as an ethanol producing pathway, during anoxia. It results in up to 70% of lactate being oxidized through the pyruvate dehydrogenase reaction and providing oxygen for fish trapped under ice or refugia (Hochachka 1980; Fagernes et al. 2017)

Physiological, fuzzy (low, medium, high), low coverage, low chance of survival

- **Biological tolerance**

Biotic interactions can change under disturbances and extreme conditions. Lack of space can increase contacts among different biota in which, avoiding predation, parasites or disease is highly important of drying survival (Crook et al. 2010).

Behavioral and physiological, fuzzy (low, medium, high), high coverage, medium chance of survival

- **Hydrological tolerance**

Ability to occupy, spawn and recruit over a wide range of hydrological regimes. Includes sub traits such as longevity (lifelong fecundity) and competitive ability (Crook et al. 2010; Hodges and Magoulick 2011).

Physiological, fuzzy (low, medium, high), high coverage, medium chance of survival

Resilience traits:

- **Mouth position**

Superior mouth orientation can enable fish to respire oxygen from surface water which in hypoxic conditions contains higher levels of oxygen than surrounding water caused by direct air contact (Graham 1997).

Morphological, categorical (superior, inferior, terminal), low coverage, low chance of survival

- **Dispersal behavior (ability)**

Refugia provides survival for fish that have no ability for aestivation. Species with wider distribution have higher chances to establish metapopulations and more sources of recolonization (Magoulick and Kobza 2003). Ability to move large distances to faster recolonize habitat after drought improves chances of drying survival. (Crook et al. 2010; Skoulikidis et al. 2011).

Behavioral, categorical (passive or active), high coverage, medium chance of survival

- **Distribution/Areal size**

As mentioned under dispersal ability, species with wider distribution have higher chances to establish metapopulations and more sources of recolonization hence provide higher chance of survival in a refuge such as isolated pool (Magoulick and Kobza 2003; Morán-López et al. 2005). Dispersal ability and distribution/areal size are two separately measured traits.

Behavioral, categorical (e.g. L(G)/M/S/E: Large areal (Global), Medium areal, Small areal, Endemic), high coverage, medium chance of survival

- **Abundance**

Abundance is negatively affected by disturbances such as drying events and as such, high abundance is a resilience trait enabling the survival of more individuals (Crook et al. 2010; Parkos et al. 2011).

Behavioral, fuzzy (or numerical/continuous), high coverage, medium chance of survival

- **Clutch size (reproductive ability)**

Temporary and unpredictable habitats are typically inhabited by organisms of high reproductive capacity which means rapid growth, early sexual maturation, and high reproductive investment (Blažek et al. 2013).

Reproductive, fuzzy (or numerical/continuous), high coverage, medium chance of survival

- **Growth rate**

Fish growth rates are decreased by high temperatures and water scarcity, and as such, fish with higher growth rates have a higher chance of survival (Griswold et al. 1982).

Physiological, numerical (average amount of weight gain per day), high coverage, medium chance of survival

- **Longevity**

Shorter lifespan means shorter time needed to repopulate the disturbed environment (Sheldon and Meffe 1995).

Physiological, numerical, high coverage, medium chance of survival

- **Ability to burrow / survive in sediment**

Moist sediment can provide refuge (Van der Waal 1998).

Behavioral, categorical – e.g. binary (yes or no), low coverage, low chance of survival

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