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# The Aquatic Metatron: A large-scale experimental facility to study the combined effects of habitat fragmentation and climate change on aquatic meta-ecosystems

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## Abstract

1. Revealing the effects of multiple global change drivers on ecosystem dynamics and functioning is a crucial endeavour, which necessitates the use of appropriate tools. Here, we present the Aquatic Metatron, a unique mesocosm facility providing a large-scale experimental resource to study the combined effects of global change components, in particular climate change and habitat fragmentation, on the ecological and evolutionary dynamics of aquatic ecosystems.
2. The Aquatic Metatron consists of 144 mesocosms of 2 $m^3$ each that can be connected to each other with aquatic corridors, and—for a subset of them—with aerial corridors. This enables effective control of dispersal across meta-ecosystems. In addition, the temperature in each mesocosm is supervised and precisely controlled, either through a heating (all mesocosms) or a cooling (72 mesocosms) system. All mesocosms can be monitored automatically for abiotic and biotic factors (pH, dissolved oxygen, conductivity, turbidity and chlorophyll *a*) allowing for long-term experimentation.
3. We tested the platform by conducting three experiments involving the manipulation of various components of global change: climate warming, biodiversity loss, eutrophication and aquatic/aerial fragmentation. The technical innovations of the platform have been validated, in particular its capacity to accurately recreate multiple climatic scenarios (e.g. heatwaves, warming, cooling) and the possibility of using aerial and water corridors to simulate fragmented landscapes.
4. The Aquatic Metatron is located in the south-west of France (https://sete-moulis-cnrs.fr/fr) and is part of AnaEE France and AnaEE-ERIC (https://www.anaee.eu/), which are large-scale research infrastructures. The Aquatic Metatron is a research facility accessible to external researchers and projects.

KEYWORDS
biodiversity, dispersal, experiments, fish, meta-communities, meta-populations, phytoplankton, zooplankton

## 1 | INTRODUCTION

Aquatic ecosystems are affected by global change, including climate change, habitat fragmentation, pollution, emerging diseases and biological invasions (Reid et al., 2019). These components of global change can alter individually and collectively ecosystem functions (e.g. biochemical cycles, productivity…) either directly, through changes in the physical and chemical properties of ecosystems, or indirectly, by reshuffling biodiversity. Understanding the processes sustaining the complex links between global change and ecosystem dynamics is urgently needed to set mechanistic models for forecasting future changes (Jackson et al., 2021) and to establish sound management plans (Haddad, 2012).

The complex relationships between the physical/chemical components of ecosystems, biodiversity and ecosystem functioning make it challenging to identify underlying causal links and requires appropriate tools. Despite the existence of statistical approaches to infer probable causalities from field observations (Grace, 2006), controlled experiments are still the gold standard (Stewart et al., 2013). Experiments allow to isolate the effects of one (or more) factor(s) on a series of response variables, while keeping other parameters constant. An increasing number of experiments manipulate more than one component of global change at a time to accurately reflect the diverse stressors faced by aquatic ecosystems and the complexity of ecological responses (e.g. Jackson et al., 2016). However, despite some notable exceptions (e.g. Davidson et al., 2015; Greig et al., 2012), most experiments are conducted under highly controlled conditions, over short periods of time and/or on highly simplified ecosystems (i.e. microcosms). However, larger, longer-term and more realistic experiments, using multiple stressor at the appropriate replication scale, are required to advance our understanding of the impacts of multiple stressors on aquatic ecosystems (Birk et al., 2020; Jackson et al., 2021). Mesocosm experiments conducted in larger apparatus under semi-controlled conditions allow for increased biological complexity and greater ecological realism (Clobert et al., 2018; Legrand et al., 2012), which is crucial in understanding the mechanisms underlying ecological responses to global change (e.g. Stewart et al., 2013; Yvon-Durocher et al., 2012).

Although mesocosm experiments allow to test interactions between global change components (Jackson et al., 2016, 2021), the ability of organisms to disperse is generally neglected. However, dispersal is a major process by which organisms can cope with global change (Travis et al., 2013). Dispersal allows organisms to move to more suited habitats and to rescue populations, both demographically and evolutionarily (Legrand et al., 2016). Movements of multiple species and inorganic matter also strongly impact the dynamics of (meta-)ecosystems, at the highest levels of organization (Leibold et al., 2004; Loreau et al., 2003). For instance, comprehending reciprocal movements of nutrients and energy across aquatic and terrestrial ecosystems is essential to understand the functioning of lotic and lentic ecosystems (Bartels et al., 2012). Habitat fragmentation, for example by dams or weirs, strongly impedes dispersal in freshwater ecosystems, ultimately limiting the ability of organisms to cope with global change, when combined with other stressors (Turgeon et al., 2019). It is likely that the technical challenge of setting experimental corridors is the main reason why dispersal is rarely considered in mesocosm experiments, especially in aquatic ecosystems where dispersal can be both aquatic or aerial (e.g. flying insects and propagules dispersed by wind or waterfowl, Figuerola et al., 2005; Havel & Shurin, 2004). Dispersal in aquatic mesocosms has already been manipulated by ‘forcing’ movements among patches, for instance by manually moving water between mesocosm units (e.g. Howeth & Leibold, 2008). However, no aquatic mesocosms have been specifically designed to explicitly address the role of fragmentation on ecological and evolutionary responses of aquatic ecosystems to global change.

Here, we present a new mesocosm facility—the Aquatic Metatron—that aims to provide a large-scale experimental resource to study the combined effects of global change (in particular climate change and (dis-)connectivity) on the ecological and evolutionary dynamics of aquatic ecosystems. We first describe the technical specificities of the platform, and we then illustrate how we can manipulate multiple components of global change and quantify various response variables. Finally, we discuss the novelty of the Aquatic Metatron compared to existing aquatic facilities and provide details on platform's accessibility.

## 2 | DESCRIPTION OF THE AQUATIC METATRON

The Aquatic Metatron is based at the ‘Station d'Ecologie Théorique et Experimentale’ located in Moulis, southwestern France (42°57′ N, 1°05′ E, Figure 1), at the foothill of the Pyreneans mountains. The climate is oceanic-like and characterized by monthly air temperature ranging from 5 to 19°C in average (with minimal around −10°C in winter and maximal around 35°C in summer) and by annual precipitation cumulating 700–1000 mm in average. An all-in-one weather sensor (WS400-UMB Smart Weather Sensor, Lufft) provides continuous measurement of ambient temperature, relative humidity, intensity, quantity and type of precipitations and air pressure. The Aquatic Metatron consists of 144 basins (Figure 1a) of 1.7 m diameter and 0.90 m height, for a water volume of 2 $m^3$ each. Such a volume allows for setting realistic trophic food chains up to small vertebrates (e.g. fish up to ~10 cm long), whereas the height of the tanks constitutes a compromise between human accessibility to the tanks (for maintenance) and the possibility for a thermal stratification to occur during warm periods in summer months. Basins can be connected to each other through transparent plexiglass aquatic corridors of 16 cm-diameter and 2 m-length to allow for aquatic dispersal (Figure 1b,c). Each mesocosm can be connected to the four neighbouring mesocosms, allowing for complex spatial arrangements such as dendritic networks (as in Carrara et al., 2012). Preliminary tests (Fronhofer et al., 2018) have demonstrated that 2-m-long corridors generate realistic movements in small fish species and molluscs, and the possibility to cumulate corridors over successive tanks allows

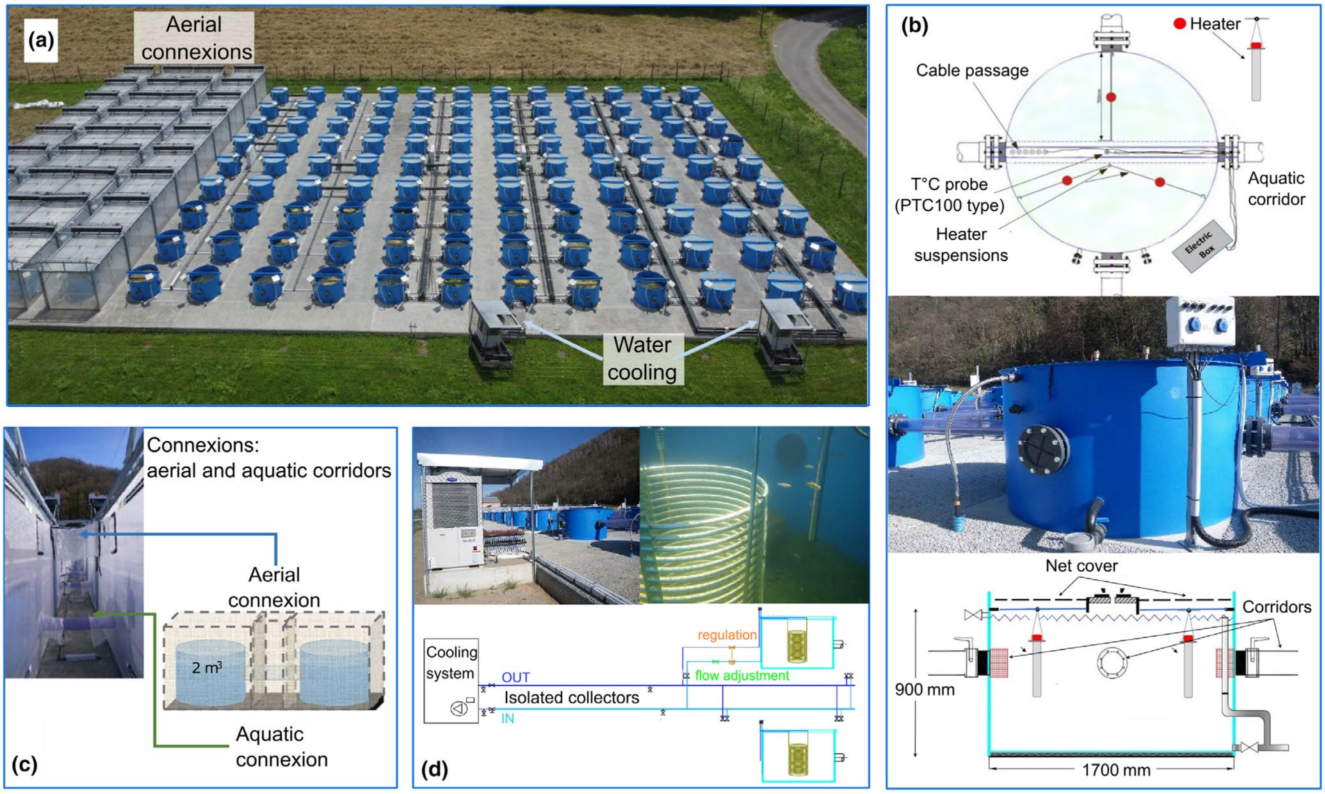

FIGURE 1 The Aquatic Metatron consists of 144 ponds of 2 m$^3$ each. (a) A general view of the platform. (b) Reservoirs can be connected to each other with aquatic corridors. The platform is connected to a monitoring station. Each pond can be equipped with heaters whose operation is directly controlled by supervision. Climatic and chemical conditions are also recorded. (c) A subset of 36 is covered by aerial mesh that can be connected/disconnected via aerial corridors. (d) Another subset has a cooling system that lowers the temperature.

for relatively long-distance movements. Filters varying in mesh size can be added at the entrance of each corridor so as to select for the size of dispersers (e.g. zooplankton can disperse, but not fish). Mesocosms can optionally be connected to each other using external pumps to allow for directional water flow within a set of connected mesocosms. An optional net covering each basin can be used to limit uncontrolled colonization of mesocosms.

Each mesocosm is equipped with a Platinum temperature sensor (Pt100 JUMO®) immersed at 50 cm depth, allowing continuous measurements of water temperature. Data are automatically recorded by a supervision system (PcVue software©). This system also supervises the heating system of each mesocosm, that is provided by three immersed heaters (Figure 1b, Schego titanium®, 350 mm, 600 W). Heating instruction for each mesocosm is programmed from the supervision system, which allows heating the mesocosms from 0 to 4°C compared to a control value (the average value of a pool of unheated mesocosms is generally used as a control), or to set each mesocosm to a reference value. This system is particularly well suited to simulate heatwaves as well as to compare ambient ecosystems to warmed ecosystems according to IPCC scenarios. Preliminary tests showed that the use of three heaters ensures optimal energy consumption and a uniform temperature in mesocosms. A subset of 72 mesocosms also has a cooling system (Figure 1d) permitting lowering water temperature. The cooling system uses chilled water units (CARRIER 30 RB026 CH®—30 kw) to supply two sets of 36 submerged exchangers of stainless-steel coil type, individually regulated by 3-way valves. Like heating, cooling regulation and instructions are set according to reference mesocosms. Another subset of 36 mesocosms are individually enclosed with removable nets made of polyethylene fabric (110 g/m$^2$, 1 mm mesh), with dimensions of 3.8 × 3.2 × 2.1 m that can be each connected/disconnected via aerial corridors (Figure 1c). Combined to aquatic corridors, this system allows to manipulate both aquatic and aerial dispersal. A roll-down textile roof system can protect against high temperatures and close automatically in case of snow risk.

The supervision system also allows for continuous and automatic monitoring of abiotic and biotic factors in each mesocosm using Modbus RS-485 connexions. Dissolved oxygen sensors (Ponsel®) can be deployed simultaneously in all mesocosms, whereas pH/ORP, RDO, Dissolved Oxygen, Conductivity, Turbidity and Chlorophyll *a* can be monitored using multiparameter probes (In-Situ Aqua-Troll®) in a smaller number of mesocosms (see Table S1 for detailed characteristics of the probes and sensors).

Mesocosms are supplied with water from the nearby Lez River (see Table S2 for water quality parameters) using a pumping and filtration system allowing to vary the level of water filtration (grain size and purity, up to UV-sterilized). Although the Aquatic Metatron has not been designed for ecotoxicological studies, some non-remanent pollutants can potentially be manipulated according to environmental concentration. Semi-automatic filling can be set on each mesocosm to maintain constant level of water across the study when needed.

Compared to other aquatic outdoor (and above-ground) lentic mesocosms, the Aquatic Metatron proves to be unique. It has the highest replication capability given the large volume of each replicate, and is—up to our knowledge—the sole facility allowing for both heating and cooling the water (Figure 2). In addition, we are unaware of any other aquatic mesocosm allowing a fine control of both aerial and aquatic dispersal.

## 3 | ILLUSTRATIONS OF SCIENTIFIC QUESTIONS AND METHODOLOGICAL POSSIBILITIES

Here, we present three research projects that were conducted as pilot studies to validate the Aquatic Metatron. Each project's scientific context and general objectives are briefly explained, and we present the technical challenges and solutions we implemented to overcome them.

Each of the project test one of the innovative characteristics of the Aquatic Metatron: the first one tests the most unique characteristic, the aquatic and aerial connexions; the second the possibility to combine connectivity and global warming in a single study and the third one presents a technically challenging innovation: warming and cooling systems allowing to reproduce a large range of climates. Each experiment has been run over a long time period (from 12 to 30 months) to show the ability of the system to sustain long-term dynamics. Results from each of these projects will be published in independent publications, and we here provide only basic details and findings.

### 3.1 | The role of aerial and water dispersal for freshwater meta-community assembly

Dispersal is an essential process with impacts ranging from genes to ecosystem dynamics. Freshwater ecosystems are often regarded as 'islands' separated from each other by hostile (terrestrial) habitats. However, many freshwater organisms can use aerial dispersal—either due to a non-aquatic stage during their life cycle (e.g. insects), or their small sizes allowing for aerial 'diffusion' (e.g. zooplankton and phytoplankton 'spores', Figuerola et al., 2005; Havel & Shurin, 2004). It is yet extremely difficult to estimate the relative roles of aerial and aquatic dispersal in meta-community dynamics. Using the specific design of the Aquatic Metatron, we tested the relative role of aerial and aquatic dispersal across a range of organisms. In a set of 32 mesocosms (Figure 3a), we designed a 'continent-island' experiment in which we applied four connexion treatments between the continent and the island: both aerial and aquatic, aerial or aquatic alone, or no connexion (each replicated four times). At the start of the experiment, the 'continent' mesocosm was inoculated with phytoplankton, zooplankton and macro-invertebrates, while the other mesocosm, the 'island', was empty of any life form (see Figure 3a; Supporting Information, Methods 1). After 30 months, all mesocosms were sampled and organisms from each compartment (phytoplankton, zooplankton, macro-invertebrates) were counted and identified. We used the taxonomic divergence between continent-island pairs as an indirect estimate of connectivity, which was measured as the Bray–Curtis index of dissimilarity. Overall, for all compartments, aquatic

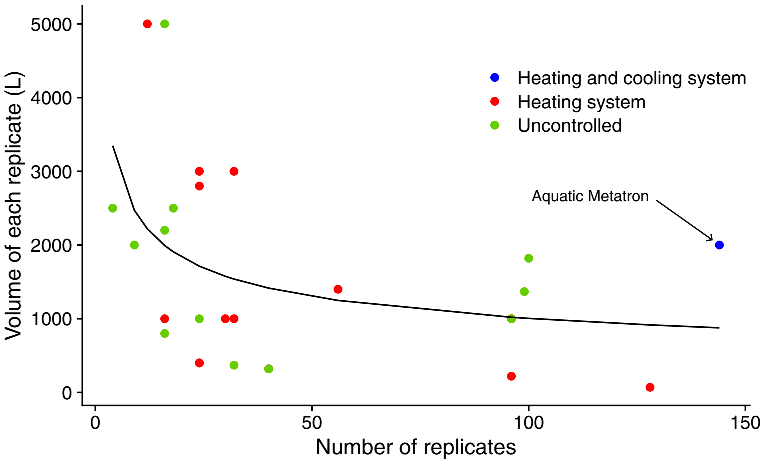

FIGURE 2 A biplot illustrating the relationship between the number of replicates (number of independent tanks) and the volume of each of them for 24 experimental facilities (dots) hosting freshwater outdoor (above-ground) lentic mesocosms from different regions of the world. In general, the higher the volume of each replicate the lower the number of replicates. For each facility, we have indicated whether the water temperature can be controlled (50% of the facilities) or not, and whether the control includes only heating or both heating and cooling. It appears that the Aquatic Metatron (blue dot) has the higher replication capability given the volume of each of its replicate. It is also the only facility allowing for both a heating and cooling control of the water temperature, which—together with the ability to control for dispersal—makes it unique. Data have been collected from https://mesocosm.org/ (accessed the 5 June 2024).

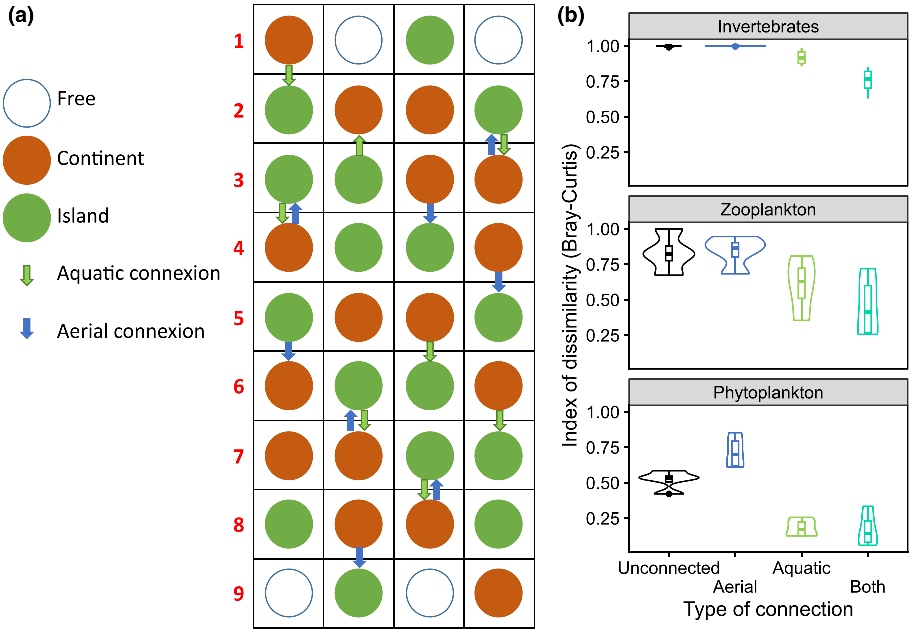

FIGURE 3 (a) Experimental design of the experiment. Continent mesocosms were inoculated with various organisms and connected (through the air, the water, both, or none) to an empty island mesocosm. (b) Taxonomic dissimilarity between continent and island mesocosms according to the connection treatments for bethink invertebrates, zooplankton and phytoplankton, respectively. The use of fish for this experiment was ethically approved by the national ethical committee under permit number #34179-2021120109429216 v5, and fish we caught according to permits delivered to SB by the Direction Départementale des Territoires.

connexion significantly allows for more similar communities between continents and islands, and combination with aerial connexion tended to reinforce similarity (especially for macro-invertebrates, see Figure 3b, see the statistics in Supporting Information, Methods 1). Interestingly, aerial connexion did not significantly change the similarity in phytoplankton and zooplankton communities compare to disconnected pairs of mesocosms (see Figure 3b), suggesting that, although weakly and for some small-sized taxon, aerial dispersal was possible through the mesh covering the mesocosms.

## 3.2 | The impact of fragmentation and climate change on meta-communities

Climate change and habitat loss and fragmentation are among the dominant factors negatively affecting biodiversity (Pereira et al., 2010). Despite the substantial progress on the ecological consequences of climatic warming and habitat fragmentation individually, there is a crucial gap in our understanding of its combined effect. To fill this gap, in May 2019, we set up an experiment in which we manipulated both temperature (ambient or +4°C warmer climate) and fragmentation in 48 mesocosms by either connecting mesocosms of the same climate treatment by groups of four through aquatic corridors or by leaving them unconnected (see Supporting Information, Methods 2). We inoculated the mesocosms with phytoplankton and zooplankton from natural surrounding lakes. After 5 months, we sampled the phytoplankton communities, and identified up to 400 individuals per mesocosm. We calculated regional (gamma) taxonomic diversity as species richness and Shannon diversity. We found regional diversity higher in isolated than in connected treatments, likely due to dispersal homogenizing connected meta-communities. Further, for the Shannon diversity index, the effect of isolation was stronger in ambient than in warm treatments, with smaller diversity values in warm treatments (Figure 4). These results suggest the importance of studying these two global change drivers concurrently as the impacts of fragmentation are modified by climate.

## 3.3 | The impact of intraspecific biodiversity loss and climate change on ecosystem functions

Climate change has a direct impact on species distribution, as well as an indirect impact on ecosystem functions (e.g. primary production, biochemical cycles) when these species are associated with these functions. Although the direct effects of climate change on biodiversity have been widely documented, this is less the case for indirect effects. More subtle indirect effects of climate change concern the loss of intraspecific diversity that can also impact ecosystem functions, as much as the loss of interspecific diversity (Raffard et al., 2019). Using the Aquatic Metatron, we set an experiment in which we manipulated both the climate and the genetic diversity of a predator fish populations (*Phoxinus dragarum*) to test for indirect effects mediated through intraspecific diversity loss. The use of fish for this experiment was ethically approved by the national ethical committee under permit number #34179-2021120109429216 v5, and fish we caught according to permits delivered to SB by the Direction Départementale des

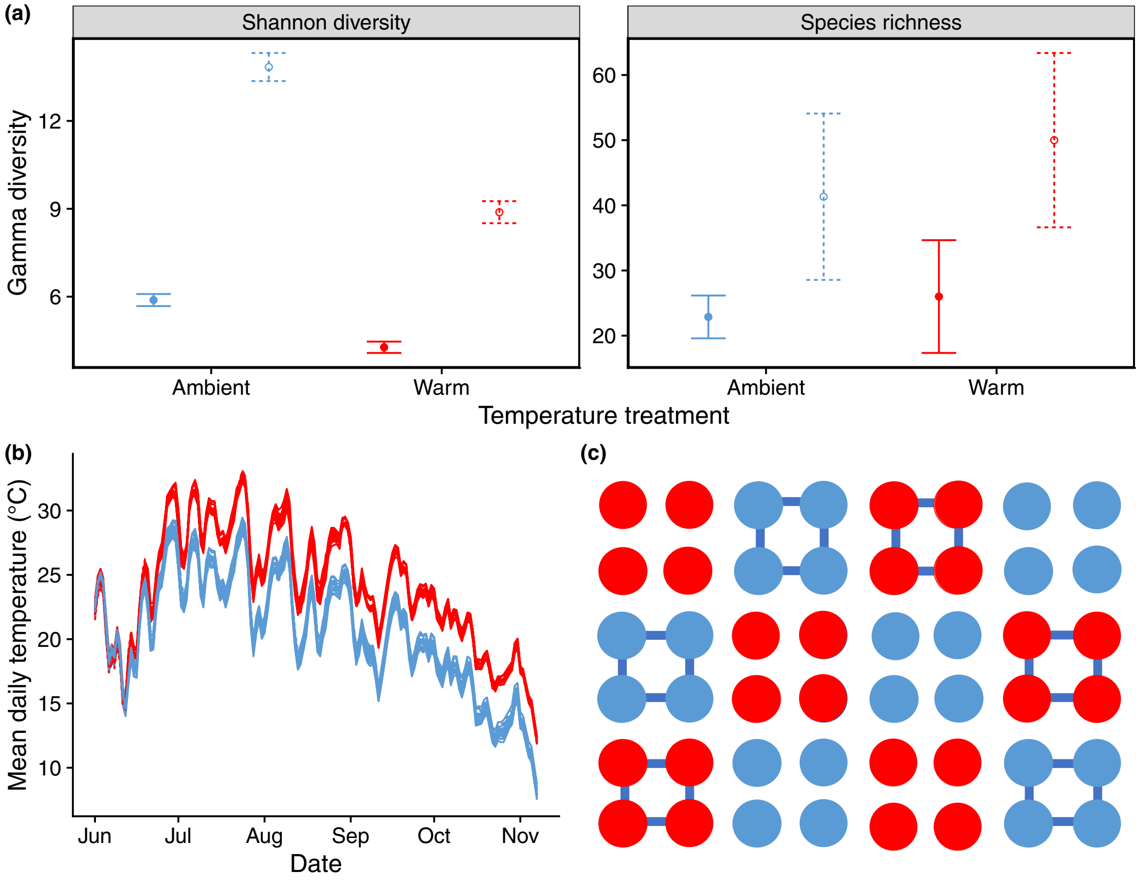

**FIGURE 4** (a) Effect of warming and fragmentation on regional gamma diversity. Mean and 95% CI of gamma diversity for species richness and Shannon diversity. Non-overlapping 95% CI indicate differences that are significant. Blue: Ambient, red: Warm, full line, filled dots: Connected, dashed line, empty dots: Isolated. (b) Temperature fluctuation in the mesocosms during the experiment (blue: Ambient, red: Warm). (c) Disposition of the 48 mesocosms during the experiment: Mesocosms were either connected by set of four or isolated, and either warmed or ambient.

Territoires. We ran a full-factorial experiment (two factors, 2 levels each: contemporary climate vs. +3°C; genetically poor vs. genetically rich fish populations, Raffard et al., 2021) with 6 replicates per treatment over a 22-months period. The main technical challenge was to maintain a +3°C difference between climatic treatments throughout the 22 months, while ensuring fish survival during the warmest months (July–August). Indeed, *P. dragarum* is a cold-adapted fish species unable to survive water temperature above ~28°C, which is commonly exceeded in mesocosms during the summer (see Figure 5). To do so, during summers 2020 and 2021, we combined the automated warming control with the cooling system (Figure 1d). To ensure that water temperature was below lethal limits all mesocosms were cooled down while maintaining the 3°C difference between mesocosms in warm or contemporary climate (see Figure 5). Thus, we observed a high summer survival as well as a positive growth rate for all surviving fish.

## 4 | DISCUSSION

We presented the technical characteristics of an open-air experimental platform aiming at studying the consequences of global change on aquatic ecosystems. Through three examples, we validated the most innovative parts of the platform and showed the range of questions that can be tackled. The Aquatic Metatron allows studying conjointly the impacts of several components of global change (multi-stress approaches). In particular, a major innovation of the platform is to allow for aerial and aquatic dispersal among sets of local habitats, which constitutes a key process for predicting the dynamics of fragmented aquatic ecosystems. Aquatic mesocosms allowing for automatic control of water temperature already exist (see Figure 2), but very few of them allow for both warming and cooling water, and even less for controlling for dispersal among mesocosms. This makes the Aquatic Metatron a unique facility that further allows for automatic long-term high frequency of several abiotic parameters (see Table S1).

Although the three experiments exemplified the technical and scientific possibilities of the Aquatic Metatron, many other questions could be tackled in this platform. For instance, mesocosm connexions can be assembled into complex architectures, making possible to study the role of landscape structure for meta-ecosystem dynamics. Furthermore, gradients of temperature (rather than dichotomic treatments) can easily be settled among sets of connected (or

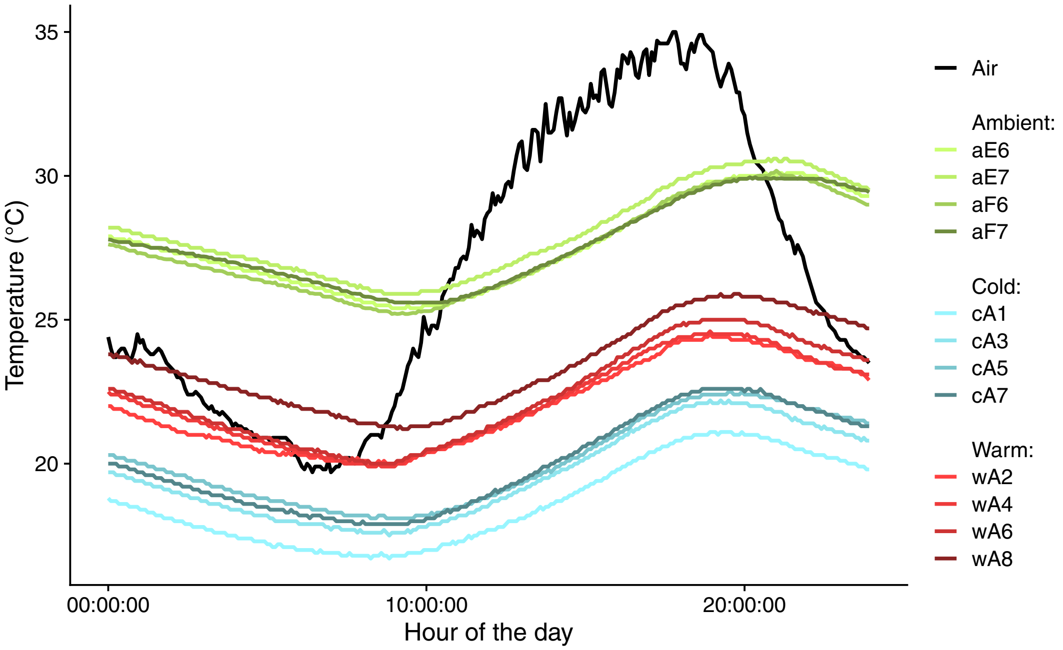

**FIGURE 5** Effect of cooling system on water temperature as a function of air temperature. 'C' denotes for cooled mesocosms (e.g. cA1), 'w' for warmed mesocosms (e.g. wA4) and 'a' for ambient mesocosms (e.g. aE6). All temperature were measured during August 2021, the warmest month of the year. Note that the warmed mesocosms are also cooled, explaining why they are on average cooler than ambient mesocosms. Mixing the cooling and warming systems during the warmest day allowed decreasing the water temperature of both warmed and cooled tanks, while maintaining a 3°C difference between the two treatments.

disconnected mesocosms). Finally, long-term studies (>24 months) can be established to study both long-term ecological and evolutionary dynamics of aquatic ecosystems (e.g. phytoplankton, zooplankton to changing environments and to dispersal). Noteworthily, the Aquatic Metatron 144 mesocosms allows the simultaneous completion of multiple experiments, as was the case with the presented projects.

Beyond the Aquatic Metatron per se, two other platforms are available and increase the experimental offer. First, a second lentic platform consisting in 90 circular mesocosms of 1100 L each and 72 smaller mesocosms of 350 L each. This simple platform (no connexion or temperature control, but biotic and abiotic parameters can be measured with stand-alone probes and sensors) is well suited for simpler experiments that require very large numbers of replicates. Second, a lotic platform consisting in 12 artificial rivers (4 m long, 45 cm depth, 30 cm width) is also available. Water level can be adjusted, river sides can be vegetated (25 cm in each side along the river), and water temperature, as well as water flow, can be controlled as in the Aquatic Metatron (same specificities). All the platforms are situated at SETE in which hosting facilities are available as well as all scientific equipment, from sample storage to genotyping and phenotyping.

The Aquatic Metatron is part of the AnaEE France and AnaEE-ERIC (https://www.anaee.eu/), which are large-scale research infrastructures that offer access to various services across Europe. The Aquatic Metatron is hence open to external researchers following a simple procedure; preliminary project proposals are submitted using a dedicated website (https://isia.cnrs.fr/), technical feasibility and mesocosm availability are then discussed with the platform managers. These co-construction with managers is essential to make the project successful and in line with the technical and scientific specificities of the Aquatic Metatron.

## AUTHOR CONTRIBUTIONS

Murielle Richard, Alexandre Garreau, Elvire Bestion, Julien Cucherousset, José M. Montoya and Simon Blanchet were involved in the conception and design of the Aquatic Metatron, Murielle Richard, Alexandre Garreau, Elvire Bestion, Julien Cucherousset, José M. Montoya and Simon Blanchet collected and analysed the data, Murielle Richard and Simon Blanchet led the writing of the manuscript. Murielle Richard, Alexandre Garreau, Elvire Bestion, Julien Cucherousset, José M. Montoya and Simon Blanchet contributed actively to the drafts and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14431.

## DATA AVAILABILITY STATEMENT

Data available via https://doi.org/10.6084/m9.figshare.26947351.v1 (Blanchet, 2024).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Supplementary material presenting the specificities of available probes and sensors (Table S1), the water characteristics of the Lez River (Table S2), methods and statistics used in experiment 1 (Supplementary Methods 1) and methods and statistics used in experiment 2 (Supplementary Methods 2).

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