# Eutrophication legacy on peri-alpine lakes ecological vulnerability to climate change

Rosalie Bruel

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# THÈSE

Pour obtenir le grade de

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Présentée par

**Rosalie BRUEL**

Thèse dirigée par **Marie-Elodie PERGA, Directrice de Recherche INRA**

préparée au sein du **Laboratoire CARRTEL (INRA, Université Savoie-Mont Blanc)**
dans **l'École Doctorale SISEO**

# Héritage de l'eutrophisation sur la vulnérabilité écologique au changement climatique des lacs périalpins

## Eutrophication legacy on peri-alpine lakes' ecological vulnerability to climate change

Thèse soutenue publiquement le **2 mai 2018**,
devant le jury composé de :

**Madame Helen BENNION**
Professeur, University College London, Rapporteuse, Présidente du jury
**Monsieur Dietmar STRAILE**
Maître de Conférences, University of Konstanz, Rapporteur
**Madame Nathalie DUBOIS**
Maître de Conférences, EAWAG, ETH Zurich, Examinatrice
**Madame Liisa NEVALAINEN**
Maître de Conférences, University of Helsinki, Examinatrice
**Monsieur Fabien ARNAUD**
Directeur de Recherche, CNRS, Université Savoie-Mont Blanc, Edytem, Examinateur

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presented by **Rosalie BRUEL**

**2 May 2018**

Thesis director:

**Pr. Marie-Elodie PERGA**
INRA, CARRTEL, France. New affiliation: UNIL, Switzerland

Members of the Dissertation committee:

**Pr. Helen BENNION**
University College London, United-Kingdom (Rapporteur)

**PD Dr. Dietmar STRAILE**
University of Konstanz, Germany (Rapporteur)

**Dr. Nathalie DUBOIS**
EAWAG, ETH Zurich, Switzerland (Examinatrice)

**Dr. Liisa NEVALAINEN**
University of Helsinki, Finland (Examinatrice)

**Dr. Fabien ARNAUD**
CNRS, University Savoie-Mont Blanc, Edytem, France (Examinateur)

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*‘We argue that the Norse Greenlanders created a flexible and successful subsistence system that responded effectively to major environmental challenges but probably fell victim to a combination of conjunctures of large-scale historic processes and vulnerabilities created by their successful prior response to climate change. Their failure was an inability to anticipate an unknowable future, an inability to broaden their traditional ecological knowledge base, and a case of being too specialized, too small, and too isolated to be able to capitalize on and compete in the new protoworld system extending into the North Atlantic in the early 15th century. […] In this respect, the seeds of the 15th century collapse of Norse Greenland were sown in the successful adaptations of the 13th and 14th centuries.’*

A.J. Dugmore et al., 2012, PNAS

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[1] http://perso.ens-lyon.fr/lise.vaudor/iterer-des-fonctions-avec-purrr/

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## ABSTRACT

Ecosystems are the complex output of both space and time constraints; their relative stability is guaranteed by feedback mechanisms, conferring them resilience towards perturbation. The presence of multiple stressors is rather the norm, but the increase of anthropogenic pressure since the 19th century is pushing many ecosystems close to their limits of resistance. The combined action of several local stresses (pollution, deforestation) makes difficult predicting the ecological impacts of climate change. It creates great uncertainties for the future of ecosystems and the services they provide (food, drinking water, biodiversity).

Our objective is to quantify the factors of the ecological vulnerability to climate warming of medium to large lakes, distributed north and south of the Alpine barrier. We question whether lake ecology is more affected by climate change depending on their exposure (are climate-driven ecological changes more pronounced in warmer lakes?) or their history of local human impacts (are climate-driven ecological changes more pronounced in lakes inheriting a long local human presence?).

We follow a paleo-ecological approach to get a long-term perspective on the system ecological trajectories, and repeatable workflow analyses. Cladocera is chosen as proxy for ecological state, while diatoms and pigments are used to infer past levels of phosphorus concentrations.

As can be seen in many other deep and large lakes over the world, we find that the studied alpine lakes display a recent history of eutrophication, dating back to the past century. We evidence asynchronous shifts at the lake scale (lag between littoral and pelagic zones). The lakes of our study are all currently undergoing restoration; however, we evidence that eutrophication has decreased the resistance of lakes to climate variability. Indeed, a longer perspective on one system, Lake Geneva, revealed two regimes of vulnerability to climate warming, before and since the onset of eutrophication. We hypothesise that even in deep systems, the littoral zone may have had in the past the potential to buffer the initial nutrient loadings, and its loss is a potential factor of vulnerability. The pelagic cladoceran assemblage is now the most sensitive to climate warming.

Over the two past centuries, local and global stakes have become intimately tied together. The degree of past perturbations explains current response to climate warming. There is a general view among the scientific community that alleviating local human forcings on ecosystems shall foster their resilience. In fact, our results indicate that restoration of large peri-alpine lakes is not sufficient to recover ecological resistance to climate variability. Local

decisions play an important role in the direction of lakes ecological response to climate warming.

Segregating the impacts of several stresses in real ecosystems is challenging, especially when the responses focus is on ecology. Our study highlights the need for statistical tools that account for bi-stability of ecosystem responses. That potential non-linearity of responses to drivers presents a challenge for quantification and forecast of the speed and persistence of ecosystem responses.

## RESUME

Les écosystèmes sont façonnés par des contraintes spatiales et temporelles. Des mécanismes de rétrocontrôles leur confère une relative stabilité, ou en d'autres mots de la résilience face aux perturbations. La multiplicité des réponses aux facteurs de stress est la norme plutôt que l'exception, mais l'augmentation des activités humaines depuis le 19$^{ème}$ siècle conduit beaucoup d'écosystèmes proche de leurs limites de résistances. La simultanéité des pressions locales (pollution, déforestation) rend par ailleurs difficile la prédiction des réponses écologiques au changement climatique. Cela génère de grandes incertitudes quant à l'avenir des écosystèmes et des services qu'ils fournissent (alimentation, eau potable, biodiversité).

Notre objectif est de quantifier les facteurs de vulnérabilité écologique au réchauffement climatique des lacs de moyennes à grandes tailles, répartis au nord et au sud de la barrière alpine. Nous questionnons si les réponses écologiques des lacs sont plus affectées par le changement climatique en fonction de leur exposition (la quantité de réponses écologiques est-elle expliquée par l'amplitude du réchauffement ?) ou de leur histoire d'impacts humains locaux (les lacs déjà soumis à de fortes pressions humaines locales sont-ils plus sensibles au réchauffement climatique ?).

Nous utilisons une approche paléo-écologique qui nous donne une perspective à long terme sur la trajectoire écologique des systèmes, ainsi que des approches statistiques et de modélisations. Les cladocères sont choisis comme indicateurs de l'état écologique, tandis que les diatomées et les pigments sont utilisés pour inférer les niveaux passés de phosphore dans les lacs.

Comme de nombreux grands lacs à travers le monde, les lacs de notre étude montrent une histoire récente d'eutrophisation, qui remonte au siècle dernier. Nous montrons des transitions asynchrones à l'échelle du lac (décalage entre les zones littorales et pélagiques). Les lacs de notre étude sont maintenant tous sur une voie de restauration, pourtant, l'eutrophisation a diminué la résistance des lacs à la variabilité du climat. En effet, une perspective plus longue sur un système, le lac Léman, a révélé deux régimes de vulnérabilité au réchauffement climatique, avant et depuis le début de l'eutrophisation. Nous montrons que même dans les systèmes profonds, la zone littorale peut avoir eu le potentiel d'absorber les charges nutritives initiales dans les lacs. L'assemblage pélagique est maintenant le plus sensible au réchauffement climatique.

Au cours des deux derniers siècles, les enjeux locaux et mondiaux ont été intimement liés. Nous montrons que le degré des perturbations passées explique leur réponse actuelle au

réchauffement climatique. Il est admis par une large part de la communauté scientifique que le fait d'atténuer les forçages humains locaux sur les écosystèmes doit favoriser leur résilience. En fait, nos résultats indiquent que la restauration de grands lacs périalpins n'est pas suffisante pour récupérer la résistance écologique à la variabilité climatique. Les décisions locales jouent un rôle important dans l'orientation de la réponse écologique des lacs au réchauffement climatique.

Isoler les impacts de plusieurs stress dans les écosystèmes réels est difficile, surtout quand les réponses se concentrent sur l'écologie. Notre étude met en évidence le besoin d'outils statistiques qui rendent compte de la bi-stabilité des réponses des écosystèmes. Cette potentielle non-linéarité potentielle des réponses aux perturbations représente un défi pour quantifier et prédire la vitesse et persistance des réponses des écosystèmes aux perturbations.

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## LIST OF ABBREVIATIONS

**AR**: autocorrelation

**DCA**: detrended correspondence analysis

**EWS**: early warning signal

**GAM**: general additive model

**PC**: principal component

**PCA**: principal component analysis

**SD**: variance

# Introduction

# INTRODUCTION

## 0.1 | MANAGING HUMAN IMPACT ON ECOSYSTEMS

Humans have contributed in shaping their environment for millennia, through modifications or exploitation of natural resources for their survival (e.g. Bajard *et al.*, 2017; Dubois *et al.*, 2017). Good management of natural resources as well as lenient conditions allowed some populations to thrive (e.g. invention of agriculture, Zeder, 2011); whereas inability to anticipate, broaden traditional ecological knowledge base, and in some cases being too specialized, too small, and too isolated, led others to disappear (e.g. Mayas, Adams, 1973; Hodell, Curtis & Brenner, 1995; deMenocal, 2001; e.g. Vikings, Dugmore *et al.*, 2012).

Since the 19th century, population growth and development of new technologies led to a great acceleration of systems interactions and the associated consequences (Steffen *et al.*, 2011). Such consequences include alterations of the fundamental biogeochemical or element cycles (carbon, nitrogen, phosphorus, sulphur, e.g. Kaye *et al.*, 2006), modification of the terrestrial water cycle through e.g. river fragmentation and soil sealing (Scalenghe & Marsan, 2009), and likely the sixth major extinction event in Earth history (Vitousek *et al.*, 1997). Climate warming is the tip of the iceberg, a metric easily quantifiable (GISTEMP Team, 2017) and passed on by medias (e.g. Abraham, 2018). The phenomenon is in many ways first-of-its-kind, by its worldwide extent (*global* change), and the inter-governmental consensus it generates outside the scientific circle (United Nations, 2015).

In fact, climate has always shown both gradual trends and unexpected rapid shifts at every latitude (high, Overpeck & Webb, 2000; low, Woodhouse *et al.*, 2010; intermediate, Woolway *et al.*, 2017). Yet, the acceleration of change brought by anthropogenic activities increases the hazards for human populations (Asian Development Bank, 2017). One of the rare certitudes is that the projected increases in carbon dioxide and temperature over the next 50 years will substantially and very rapidly exceed the conditions under which the Earth has been developing over the past millennia (Meyer *et al.*, 2014). The effects of climate change are already recorded at every organisation level, from gene to ecosystem (Scheffers *et al.*, 2016).

In response to climate change and since the 1950s, scientists and non-profit organisations have urged the governments to reconsider their management decisions to accommodate economic growth with biodiversity and ecosystem benefits preservation in a changing world (Epple & Dunning, 2014). Indeed, biodiversity and healthy ecosystems play an important role in helping people to adapt to climate change (Colls, Ash & Ikkala, 2009). Solutions brought by healthy ecosystems include natural barrier against disasters, shelter, and provision of drinking water and food. In the socio-ecological field, these ecosystem benefits are referred to as ‘ecosystem services’ and gained attention when the first estimates of their monetary value were carried out (Westman, 1977; Costanza *et al.*, 1997). Working on natural solutions is rewarding because the means are readily available and cheaper to maintain in the long-term than engineering-based solutions (Few, 2003; Colls *et al.*, 2009; Fisher *et al.*, 2014; Sumaila *et al.*, 2017). However, local human impacts alone (such as light pollution e.g. Hölker *et al.*, 2010), are known to be major disrupters of both biodiversity and habitat heterogeneity. In other words, human activities may sabotage the resilience potential of ecosystems (see Box 1, Box 2).

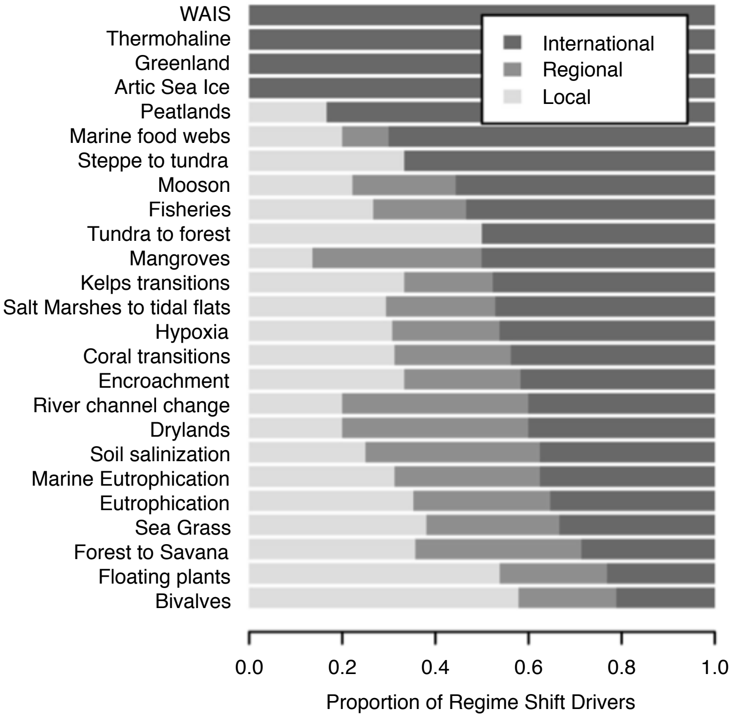
**Box 1.** Local versus global forcing.

Ecosystems are shaped by a certain number of drivers (see Chapter 1 for more details on the notion). These drivers can have a local or global origin. Deforestation, point source pollution, nutrient inputs and hunting are examples of local drivers. Global drivers include rise of sea level, greenhouse gas emissions, and change in sea surface temperature.

The presence of several and simultaneous forcing increases the risk of regime shifts in ecosystems. However, two thirds (62%) of the identified drivers have the potential to be managed locally or nationally, while one third can only be managed at the international scale (Rocha *et al.*, 2015). This seems to imply that reducing local and regional drivers can prevent many risks of climate change.

The concepts of global and local stressors are at the core of this study.

**Legend** │ Managerial opportunities per regime shift. Each bar shows the proportion of drivers that can be managed at different scales (International – dark grey; Regional – grey; Local – light grey). Source: Rocha *et al.* (2015).



As local and global stakes have become intimately linked, there is a popular view suggesting that alleviating local human forcing on ecosystems should foster their resilience (Box 3, capacity to resist, recover or adapt) to climate change (Scheffer *et al.*, 2015; Rocha, Peterson & Biggs, 2015). Yet, the ubiquitous and simultaneous facets of human impacts seriously hamper our ability to provide evidences of such mechanisms based on contemporary monitoring data. In fact, some empirical observations on coral reefs show that their resistance to the symptoms of climate change (ocean acidification, higher water temperature) is higher where local stressors already excluded disturbance-sensitive taxa than in marine reserves, or when two stressors mitigate each other (Côté & Darling, 2010). Indeed, the idea that reducing one stressor will benefit the ecosystem only holds if this stressor and climate change have additive or synergetic effect *i.e.* their combined impact is the sum of / greater than their impacts taken separately. However, 43% of interactions between stressors have an antagonist effect *i.e.* their combined effect is lesser on the studied organization level (population, community) than the sum of each stress taken separately (assessment for marine systems, Piggott, Townsend & Matthaei, 2015). In such a situation, the two stressors mitigate one another. Reducing only one stressor can either have little effect or worsen the impacts of the second stressor (Brown *et al.*, 2013).

The outcomes specific to the three scenarios of interactions (additive, synergetic and antagonistic) are illustrated in Figure 0.1, where each point is a species with randomly generated tolerances to local (y-axis) and global stressors (x-axis). Species were assigned a score of tolerance. Tolerance, or vulnerability (Box 3), is the amount of change observed compared to a control treatment. Control treatments are used in experimental biology to define the baseline for natural variability. For instance, if we are testing the number of abnormal development in a coral in response to salinity levels, the control treatment should monitor for the same period the abnormal development of coral with seawater (optimum conditions). Species found in the white zone are those weakly affected by either stressor; species in the dark grey area are those strongly affected by climate (global forcing). Species in the light grey area are those affected both by local and climate stressors. Antagonistic effect of stressors (Figure 0.1-C) increases the proportion of species found in the white zone on the graph, which is the zone for which no effects are found for either stressor.

For instance, there is an antagonistic effect of lower salinity paired with higher temperature (two expected outcomes of climate warming in marine environments) on coral reefs (Crain, Kroeker & Halpern, 2008; Li *et al.*, 2009; Chui & Ang, 2017). Indeed, lower salinity increases the abnormal embryonic development of the coral *Platygyra acuta,* while higher temperature increases its settlement success (Figure 0.2). Herein, one symptom of climate change is counteracted by another (Chui & Ang, 2015, 2017). To sum up, managing ecosystems in a context of climate change requires flexible management practices depending on the ongoing research and ecosystems (or communities or species) specificities (Mumby *et al.*, 2017). Moreover, the commonly accepted idea that reducing some locally manageable impacts should foster resilience to climate change may not be true for some interactions (antagonist).

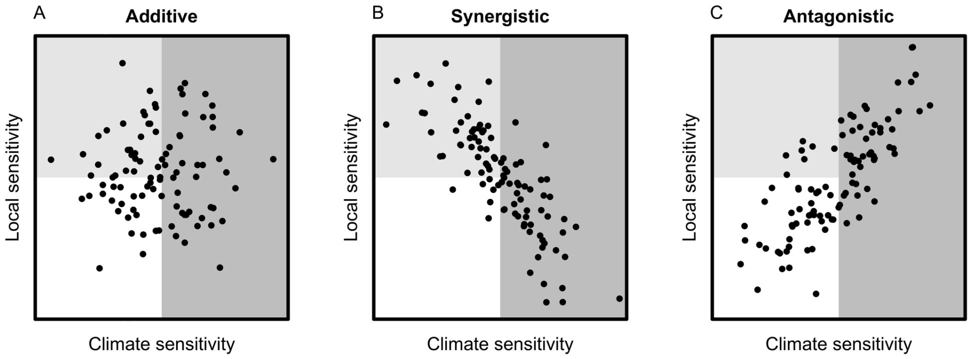


**Figure 0.1** I Co-tolerance of species to both climate and local stressors for three types of interactions A) additive, B) synergetic and C) antagonistic.

Species tolerances were generated randomly by Brown *et al.* (2013) (nominal scales) for an additive interaction (random co-tolerance, ρ = 0), a synergistic interaction (negative co-tolerance, ρ = -0.8), and an antagonistic interaction (positive co-tolerance, ρ = 0.8). Each point represents the tolerances of a single species to the two stressors. Species in the dark grey region will be threatened by climate change stress, the local stressor will additionally affect species in the light grey region, and species in the white region will be unaffected by either stressor. The most species will be lost with a synergism and the least with an antagonism. Source: Brown *et al.* (2013).

Another challenge faced by ecosystems managers lies in the complexity of fitting models for ecological processes, simply due to the number of drivers impacting any biological variable. Models are originally based on mathematical assumptions, and the best forecast models rely on emergent statistical properties of data to make short-term projections. For instance, physical models can be applied with high precision because the first principles of physics are well defined. Biological models, in contrast, inherently rely on a broad set of parameters. For instance, fish populations do not systematically experience consistent rates of birth, death, growth, or movement (Schnute & Richards, 1995). Assuming that the process is stable leads to a process error (Schnute & Richards, 2001). Furthermore, biological metrics may suffer from measurement errors because the sampling takes place in different or difficult conditions, where a perfect sampling strategy may not always be feasible (as somehow reflected by the number of sampling methods, Lapointe, Corkum & Mandrak, 2006). Running models on small datasets increases the risk of missing an important part of the equation due to biases introduced by either processes or measurements errors. Process and measurement errors are an issue whatever the dataset size, but a small sample size increases the statistical reliability problem. On the other hand, a larger dataset helps securing the quality of model predictions (Schnute & Richards, 2001). The problem posed by models fitted on too little data is best illustrated by the collapse in the 1990s of various important fish stocks. Quantitative stock assessment methods and mathematical models did not guaranty the sustainability of fisheries (Schnute & Richards, 2001). Models that failed to predict systems trajectory most likely suffered from the substantial uncertainty linked to the non-stationarity of other physical, chemical and biological parameters playing out across large space and time scales (Garcia & Cochrane, 2005; Schindler & Hilborn, 2015). In other words, the complex interactions between stressors (i.e. additism, synergism, antagonism, Folt *et al.*, 1999; Piggott *et al.*, 2015) can also affect the temporal scenarios. In that respect, ecosystem approaches, as opposed to single parameter models (Garcia & Cochrane, 2005), and long-term datasets (Spears *et al.*, 2017) are possibly the only way to achieve an objective probability framework.

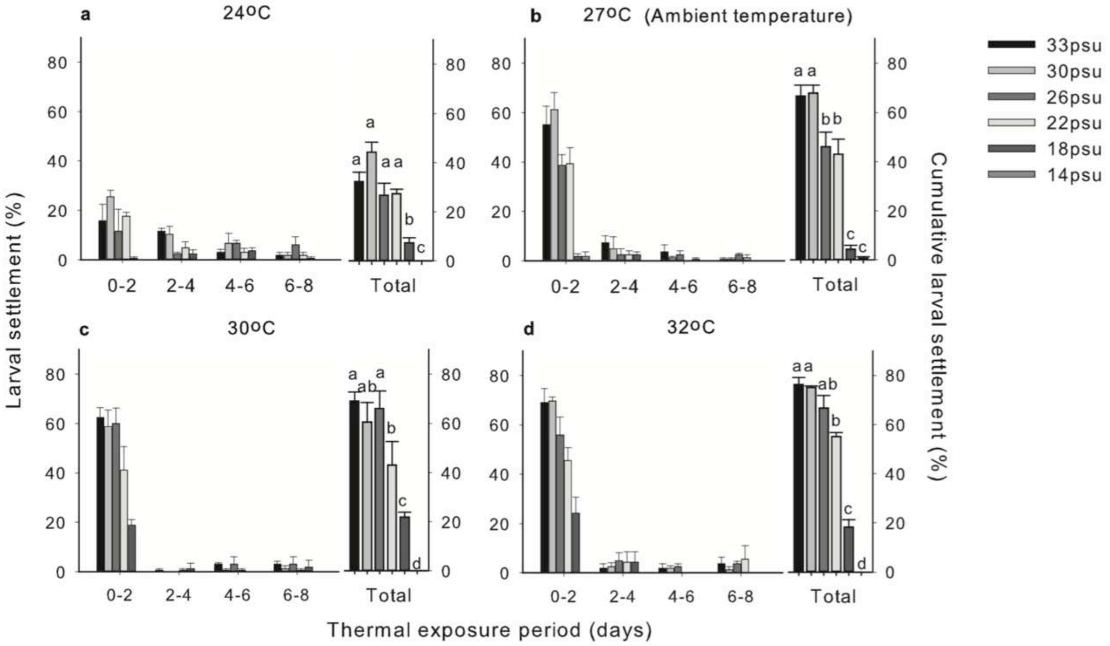


**Figure 0.2 I** Mitigation effect of temperature on salinity stress for the settlement of *Platygyra acuta* larvae. Mean (+SE) percentage (%) and cumulative surviving settlers from Chui *et al.* (2017), in response to different temperature and salinity treatments ($n = 3$ replicates per treatment). Data indicated with the same letter showed no significant difference in settlement success (Two-way ANOVA, $P > 0.05$). With increasing temperature (from a to d), the larval settlement success increases for every concentration of salinity.

Usually, models extrapolate linearly into the future, which – according to an abundant research – is valid only inside a limited range of parameter variations (Scheffer & Jeppesen, 1998). Indeed, there are a number of internal feedbacks that help maintaining a system in a stable state. However, above a given threshold, the strength of the stressor may override these feedbacks, and the system may be pushed in an alternative stable state. In other words, typical models assume linear functions, while actual behavior of biological variable is generally better described by step functions. This is what lies beyond the concept of regime shift (Rocha *et al.*,

2015) (more details in Chapter 1). In the alternative regime, or stable state, new feedback mechanisms stabilize the system, which make the recovery *i.e.* the return to initial stable state or regime more difficult. This resistance to recovery generates a 'recovery debt', evidenced in a variety of Earth ecosystems (Moreno-Mateos *et al.*, 2017). The recovery debt characterizes a period during which biodiversity and ecosystem functions (carbon and nitrogen cycling) are lower than before the perturbation, even if the initial driver was completely removed.

**Box 2.** Healthy mangroves as a natural way to lower the impacts of climate change.

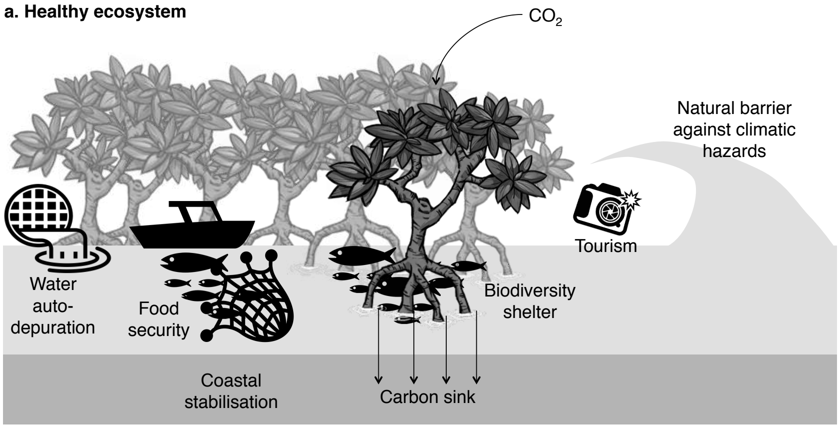
Mangrove forests (and other coastal wetlands such as tidal marshes and seagrass meadows) are valuable long-term carbon sinks. They are storing carbon in the plants themselves, but more importantly, in the soils below for hundreds to thousands of years. They have an uptake ratio of up to five times the one of a terrestrial forest (Alongi, 2012). Alongside, they provide other important ecosystems services including coastal protection, biodiversity and food production (Colls *et al.*, 2009).

As such, they are a good example of how healthy ecosystems are beneficial to populations at the local and global scale. Other coastal and marine ecosystems (e.g. coral reefs, kelp forests) do not present such carbon sequestration potential. While the role of marine phytoplankton in the sequestration of carbon in the oceans is of great importance (Sabine *et al.*, 2004), it is a lot more difficult to manage biota of deep oceans in remote and worldwide distributed oceans. On the other hand, coastal wetlands are readily accessible, hence more easily managed. For instance, policy and decision makers invest in 'coastal blue carbon' to meet international greenhouse gas commitments by launching conservation and restoration programs on mangroves (Siikamäki, Sanchirico & Jardine, 2012).

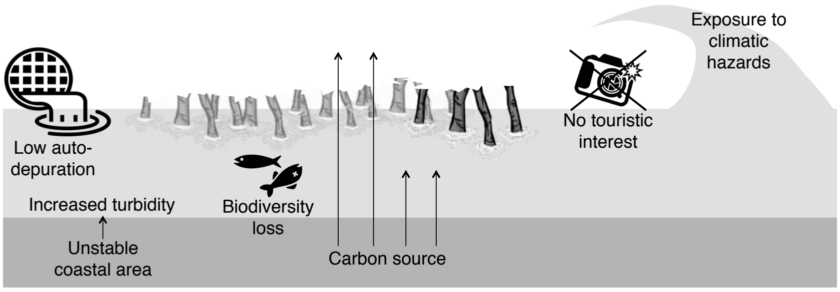
However, extensive areas of coastal wetlands are lost every year (Valiela, Bowen & York, 2001). When these ecosystems are converted to other uses or degraded, they turn from net carbon sinks into carbon sources as much of the carbon stored in the soils beneath them is released back into the atmosphere and ocean (Pendleton *et al.*, 2012).

**Legend** | **(a)** Healthy mangrove forests, providing a range of local ecosystem services such as water depuration, food security, coastal stabilisation, biodiversity shelter, tourism, as well as natural barrier against climatic hazards. Mangrove forests play a global role as an important carbon sink. **(b)** Degraded mangrove forest no longer providing ecosystem services. The ecosystem switched from being a carbon sink to a major carbon source to the ocean and the atmosphere.

**a. Healthy ecosystem**



**b. Degraded ecosystem**



**Box 3.** Glossary of resilience.

**Recovery:** Captures the endogenous processes that pull the disturbed system back towards an equilibrium (Hodgson, McDonald & Hosken, 2015)

**Resilience:** The capacity of a system to persist or maintain function in the face of an exogenous disturbance (Holling, 1973; Hodgson *et al.*, 2015)

**Resistance:** The instantaneous impact of an exogenous disturbance on system state (Hodgson *et al.*, 2015)

**Vulnerability:** Also called sensibility, and defined as the opposite of resistance. It is the degree of changes in an ecosystem state that can be attributed to a given disturbance.

## 0.2 | LAKES AS SELF-ARCHIVING SYSTEMS MODEL

We worked on lake ecosystems in order to assess whether vulnerability of ecosystems to climate change can be altered by local human impacts. Lakes represent 'aquatic island', relatively isolated and easily quantified and manipulated ecosystem (Carpenter *et al.*, 2011; Spears *et al.*, 2017). Moreover, their sediment preserve traces of past environments (Smol *et al.*, 2001; examples reviewed in Dubois *et al.*, 2017), which makes them excellent candidates for palaeostudies. Deep lakes, in particular, display a good sequential sedimentation which provides an opportunity for high-resolution palaeo-ecological reconstruction (Perga *et al.*, 2015).

Lakes (and inland waters in general) are among the challenged resources, as they fulfil basic needs for humans and wildlife. Resources are limited and unequally distributed throughout the world. They provide several ecosystem services both intrinsic and human-valued (Kankaala *et al.*, 2016). The category of intrinsic services embodies the habitat for freshwater biota and the role of regulating water flows (e.g. through changes in volume) and water quality (e.g. by facilitating sedimentation). Human-valued services encompass production of drinking water, fishing, sewage disposal, and tourism. Moreover, because lakes receive water from their catchment, there are indirect modifications in land-use that indirectly rely on or impact lakes, including vegetation clearance, farming, and urbanism.

The main threat on lakes worldwide is undoubtedly eutrophication (Smith, 2003), which is the process of water enrichment with nutrient as a consequence of human activities leading to excessive algal growth (Hutchinson, 1973). In short, there are two types of eutrophication history. For most lakes having undergone recent eutrophication (past 100-200 years at most), sediment records keep track of the start and the probable cause of the process (e.g. Lake Bourget in the French Alps, Capo *et al.*, 2016). On the other hand, many lowland lakes have been on a continuous eutrophication journey for the past millennia. They face a different context *i.e.* they have a long history of human settlement and agriculture development (e.g. Lake Igaliku in Greenland, Capo *et al.*, 2016). Successful abatement of in-lake phosphorus was achieved in most lakes in central Europe, which belong to the former type of lakes (recent eutrophication history). However since the late 20th century, climate warming is raising concerns amongst lake managers. Climate change may mimic the symptoms, hence the consequences of eutrophication (Moss *et al.*, 2011). The consequences range from bottom water hypoxia (Jenny *et al.*, 2016) to the appearance of toxic cyanobacterial blooms (Kosten *et al.*, 2012; Taranu *et al.*, 2015). In fact, lakes are responding to atmospheric warming, one of the main component of climate change, through a set of direct and indirect processes (Figure 0.3).

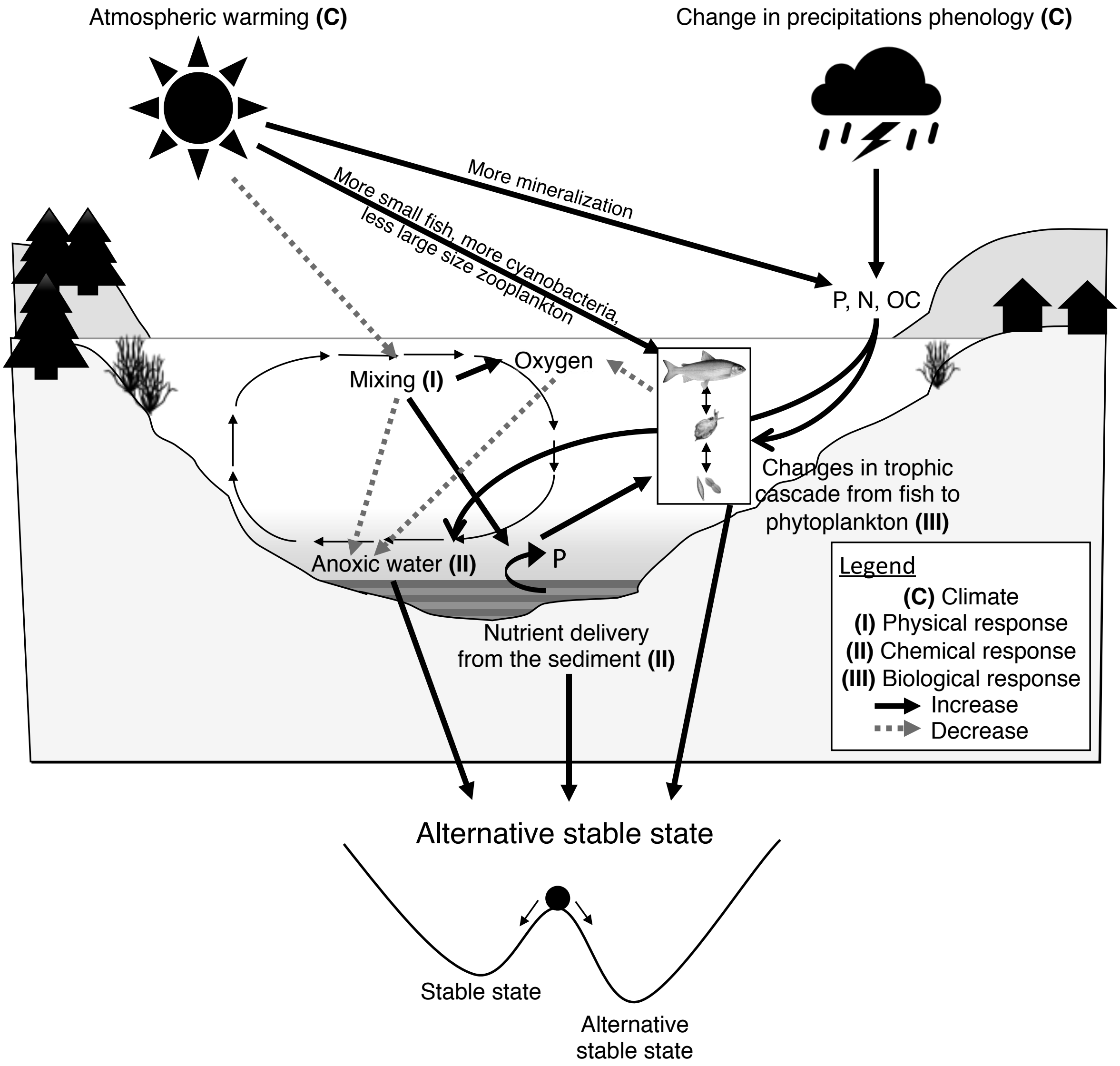


**Figure 0.3 I** The complex interactions between climate and the different levels of responses i.e. physical (I), chemical (II) and biological (III).

Because of the internal feedbacks (e.g. more mixing decrease the volume of anoxic water, but warmer climate decreases mixing which may in turn increases the volume of anoxic water), the possibility for alternative stable state is high. Redrawn mostly from Moss *et al.* (2011).

Briefly, atmospheric warming is supposed to increase the mineralization of nutrients and organic carbon (Gudasz *et al.*, 2010), whose loadings to the lakes are also expected to increase due to a change in precipitation dynamics (higher frequency of extreme events). More nutrients will directly impact the algae growth in lakes, which in turn will increase sedimentation of organic matter. More accumulation of organic matter is likely to trigger higher oxygen consumption in deep waters. Atmospheric warming through reduced water mixing will reinforce deep-water oxygen depletion. Deep-water anoxia increases phosphorus release from sediments, which in turn contributes to algae growth. The old paradigm stating that an ecosystem will always recover from local perturbations is no longer credible considering the high diversity of lakes internal feedbacks (Folke *et al.*, 2004). They suggest instead a high potential for alternative stable states: the existence of more than one steady state.

The similarity between eutrophication and climate change impacts on freshwater bodies, as well as the fact that they can reinforce each other (synergism), has at least two important management consequences. The first one concerns the diagnosis on restoration success. Indeed, the fact that some systems resist restoration could just come from a new baseline brought by climate warming (Battarbee *et al.*, 2005) (Figure 0.4). Under the ‘new baseline’ hypothesis, we would need to learn to live with ecosystems that may not be able to revert to the past production of ecosystem services (Figure 0.4). The second consequence of additive or synergetic climate change and eutrophication is that the current levels of local perturbations that ecosystems can bear may become lower under future climatic scenarios. The concept of ‘safe operating space’ has been first defined by Rockström *et al.* (2009b). They identified nine planetary boundaries that should not be crossed to preserve human development. They involve systemic processes on a planetary scale, such as climate change and ocean acidification, as well as aggregated processes at the local or regional levels, such as freshwater and land use changes, loss of biodiversity, and chemical pollution. The message is that any process should be studied at the adequate scale to prevent any catastrophic, permanent shift. The concept finds echoes at the ecosystem scale, if eutrophication and climate change have additive or synergetic effects (Figure 0.5). Indeed, as the climate is warming (stress increases along the y-axis), systems are more likely to shift away from their safe operating space (the grey zone in Figure 0.5) for lower levels of local human impact quantified on the x-axis (Scheffer *et al.*, 2015). Again, these conclusions need to take into consideration possible multi-stressors interactions (Folt *et al.*, 1999; Piggott *et al.*, 2015), and only apply to forcings with additive or synergetic effects.

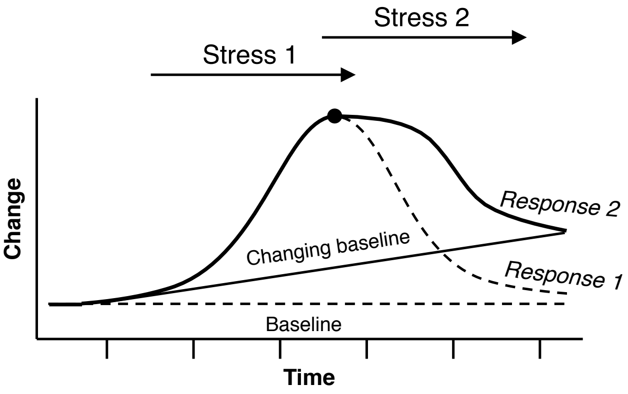


**Figure 0.4 I** Idealised diagram illustrating decadal-scale change from the past to the future.

It is designed to show the response of a lake system to increasing and decreasing stresses and the potential change in targets for ecosystem recovery resulting from a change in the boundary conditions (e.g. climate) of the system**.** Reproduced from Battarbee et al. (2005).

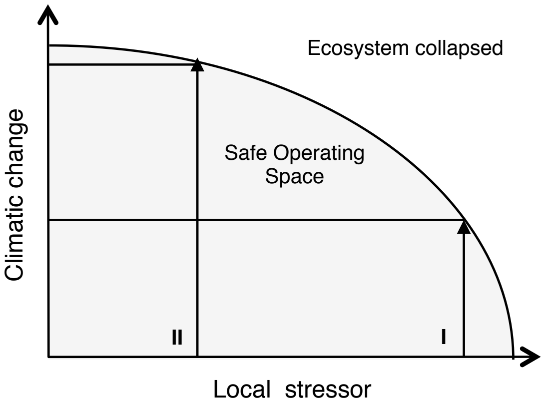


**Figure 0.5 I** Schematic representation of safe operating space.

In ecosystems at risk of collapse, safe boundaries for local stressors, such as harvest rates or pollution, often change with climate change. A local stressor that is currently at a safe level (I) needs to be adjusted to a lower value to keep the system within the safe operating space in a future climate (II). Reproduced from Scheffer et al. (2015).

In summary, lakes are good exploration fields to investigate the impacts of several stressors (local and global) with a long-term perspective, thanks to their self-archiving capacity. We focused our study on one geographic zone, the peri-alpine area (around the French, Swiss, and Italian borders), for several reasons. First, central Europe is a place of intense development, with pronounced human development over the course of the 20th century (Romano & Zullo, 2013). Second, air temperature has risen twice as fast in the alpine region than at the global average (Figure 0.6). Should global warming have an impact on lakes, the consequences are expected to be more pronounced in the peri-alpine area.

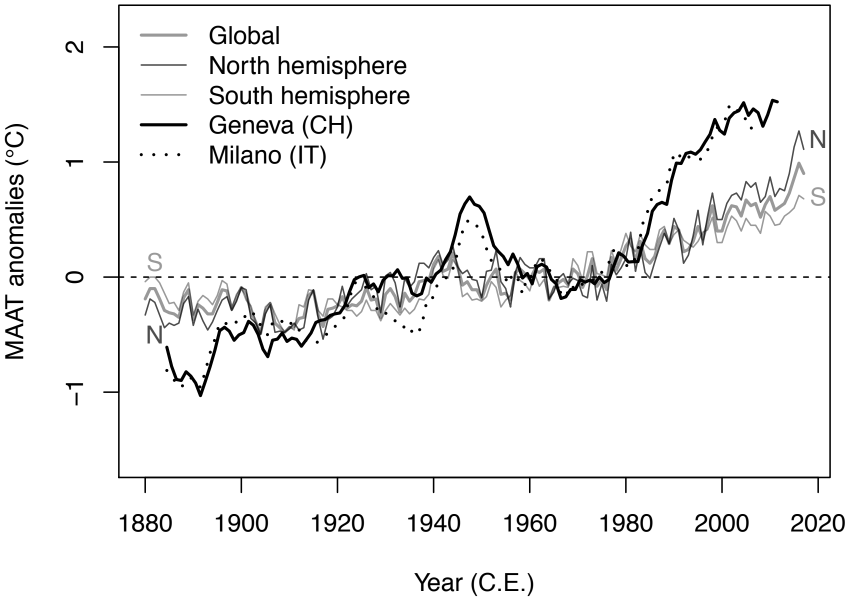


**Figure 0.6 I** Mean annual air temperature (MAAT) anomalies.

Global MAAT (thick grey line) anomalies; Northern and Southern hemisphere MAAT (thin grey lines); MAAT (moving average over a 10-years window, thick black line) at the Geneva Cointrin Weather station (CH); and MAAT (moving average over a 10-years window, thick dotted black line) at the Milano Weather station (IT) for the 1880-2017 period. Global and hemisphere MAAT were retrieved from the Goddard Institute for Space Station website (Hansen *et al.*, 2010; GISTEMP Team, 2017). Elimination of outliers and homogeneity adjustment was carried out on the GISS dataset by the authors. All temperature anomalies were calculated for the basis period 1951-1980. For Geneva station, monthly temperatures were retrieved from the MeteoSwiss database and a yearly average (January to December) was computed. Data from Milano station were retrieved from the HISTALP database (Auer *et al.*, 2007).

## 0.3 | MAIN QUESTIONS AND THESIS OUTLINE

Aside from the research on the causes and dynamics of climate change, managing its impact has become a burning subject. The study of vulnerability (originally, the measure of damages undertaken by a system resulting from its exposure to a perturbation) is a concept that emerged in risk assessment sciences. Its adoption by the Intergovernmental Panel on Climate Change, as a way to evaluate the susceptibility of a system to change due to climate forcing, helped the propagation of the concept in many studies, notably in the socio-ecological field (Gallopín, 2003; Turner *et al.*, 2003; Adger, 2006; Gallopín, 2006; Smit & Wandel, 2006). The outcome is clear and has been mentioned above: climate change is impacting all types of aquatic and terrestrial systems, modifying the genes, the morphology, the phenology of species (Scheffers *et al.*, 2016). But a parallel observation is striking: biological responses to changing climate are complex and rather unpredictable at large scales (Dokulil *et al.*, 2010). Figure 0.7 illustrates the cascading (from high to low) degree of coherence (expressed as correlation coefficients) of several group metrics (physical, chemical, nutrients and biological) across six lakes from the same region. This pattern can be explained by a layering of parameters (Figure 0.8) gradually modulating the impact of change in climatic factors on lakes (Livingstone *et al.*, 2010).

In fact, the coherent response of lake surface water temperature in morphologically dissimilar lakes in different geographical regions demonstrates that large-scale climatic forcing on broad timescales is really important for lakes (Livingstone & Padisák, 2007; Livingstone *et al.*, 2010). The rate of lakes warming depends on local characteristics rather than the region, as the most rapidly warming lakes are widely geographically distributed (O'Reilly *et al.*, 2015). In that respect, a simple model with the correct configuration (mainly morphometric parameters) requires air temperature as a unique input variable to describe intra- and inter-annual variability in a various range of low-altitude lakes (Piccolroaz, Toffolon & Majone, 2013; Toffolon *et al.*, 2014).

Chemical parameters, on the other hand, will be locally affected by the local geology and land cover (Nilsson & Håkanson, 1992). In fact, the relatively high coherence among chemical parameters depicted in Figure 0.7 could also be explained by the fact that the sampled lakes are all located in the same region, the Austrian Alps. Nutrients are even more highly linked to the occupation of the watershed (Battarbee *et al.*, 2005).

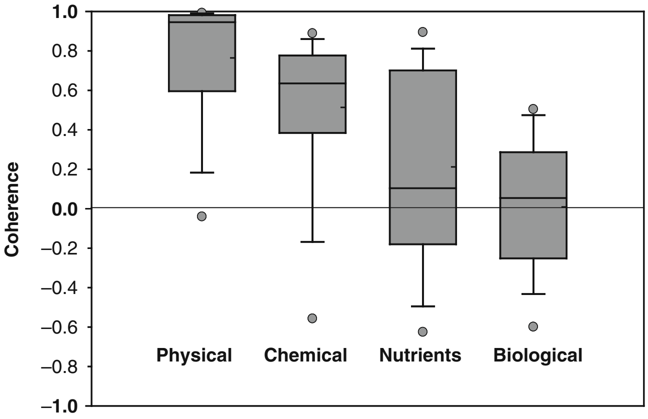


**Figure 0.7 I** Regional coherence between pairs of six Austrian alpine lakes (from Dokulil & Teubner, 2002; Dokulil *et al.*, 2010).

Box limits indicate the 25th and 75th percentiles., whiskers are the 10th and 90th percentilesm and the solid line is the medium. Physical responses include surface temperature, light attenuation and Secchi-depth. Chemical responses are pH, conductivity and oxygen concentration. Nutrients are a measure of total phosphorus, total nitrogen and dissolved silica. Biological responses are chlorophyll a and phytoplankton biomass.

Finally, the effects of climate change on lake biology are complex, difficult to disentangle from other influences, and not easy to generalise (Dokulil *et al.*, 2010). One of the problems when comparing biological responses is to pick a relevant proxy. Indeed, chlorophyll a and phytoplankton biomass selected in Dokulil *et al.* (2010) are strongly impacted by local land use and fluxes of nutrients to the lake.

If regional patterns cannot explain lakes vulnerability to climate change, then what does (Figure 0.8)? Here, we try to bring some insights on that question. We argue that temporal perspective is equally important as spatial perspective to understand ecological responses to climate change (Wohl *et al.*, 2014; Wolkovich *et al.*, 2014).

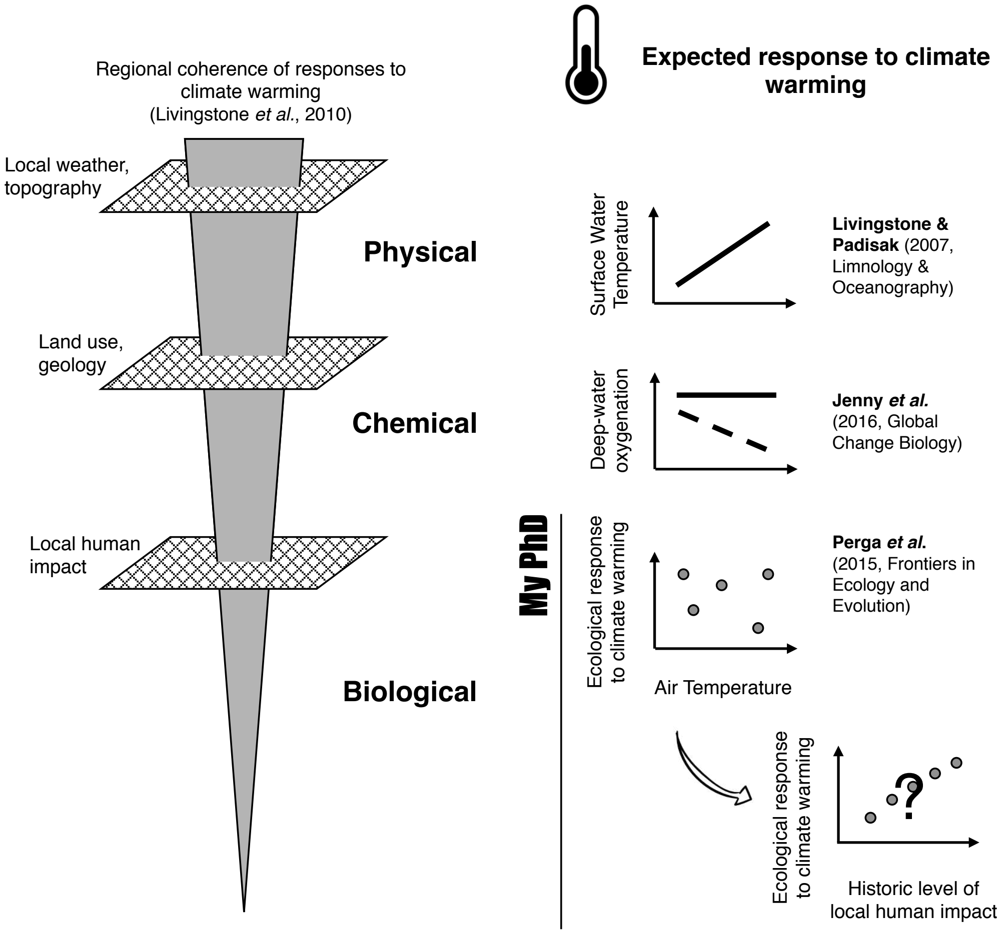
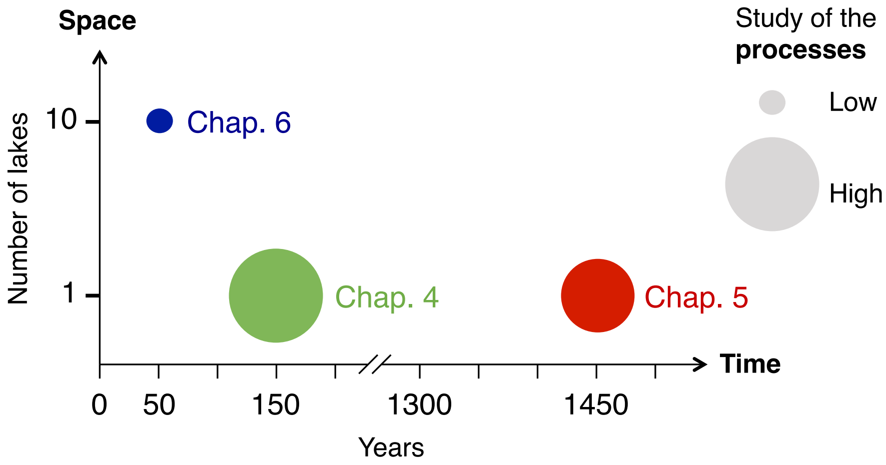


**Figure 0.8 I** Several filters decrease the regional coherence of responses among lakes.

While lake surface water temperature is highly coherent with air temperature, the chemical responses are more complex and may be modulated by the local history of human impact (Jenny *et al.*, 2016). The biological responses are complex and cannot be explained by the rate of warming of lake water. One of our hypotheses is that the historical level of local human impacts increases lakes vulnerability (i.e. amount of responses) to climate change.

Firstly, we investigated the responses of deep lakes to multi-stressors (Figure 0.9 question 1). As mentioned above, the lack of restoration in some deep lakes has sometimes been attributed to concomitant effects of climate change (Figure 0.4). Alternatively, the multiple feedbacks in lake-ecosystems create a high potential for alternative stable states (Figure 0.3). The transition from one state to the other takes place above or beneath a critical threshold, according to the concept of regime shift (see Chapter 1 for details on mechanisms). In such cases, tools to isolate the individual contribution of each stressor are needed. We tested the potential for regime shift in a medium-sized peri-alpine system in northern Italy, Lake Varese, which underwent dramatic changes in the second half of the 20th century due to eutrophication. Despite many restorations efforts outside and within the European Water Framework Directive (Zaccara *et al.*, 2007), the lake still suffers from deep-water anoxia and seems to resist further restoration efforts. As a result, the system presented an ideal context for testing regime shift hypotheses.



1) How are deep lakes responding to multi-stressors? Are those responses linear? ➔ In depth processes
2) Does local human impact increase lake vulnerability to climate variability? ➔ Long-term approach
3) What are the drivers of lake responses to climate change? ➔ Spatial approach

**Figure 0.9 I** The three research questions addressed in this thesis.

(1) Different levels of investigations were required to investigate in depth the way deep lakes are responding to multi-stressors. (2) A long-term perspective on one lake shed light on the regime of vulnerability to climate variability of deep lakes. (3) A spatial approach to question what makes some systems more vulnerable to climate than others.

Secondly, we assessed whether we could apprehend lake vulnerability to climate variability by going back in time before the rise of human impact, i.e. before the 20th century (Figure 0.9 question 2). In other words, we tried to identify the changing baseline conceptualized by Battarbee *et al.* (2005, Figure 0.4). In practice, we worked on the ecological state evolution of a deep, well-studied lake (Lake Geneva), and reconstructed its ecological state over the past 1,450 years. Monitoring data support the hypothesis that the system is now responding to climate change (Anneville, Gammeter & Straile, 2005; Anneville *et al.*, 2009). However, some effects may also be due to local human impact. To summarize, we tested whether Lake Geneva displayed several regimes of vulnerability to climate variability.

Finally, after evidencing processes in the two aforementioned systems, we investigated the reasons why some systems are more vulnerable to climate warming (Figure 0.9 question 3). To do so, we worked on twelve peri-alpine lakes, evenly located North and South of the Alpine barrier, distributed along large size and eutrophication gradients. The objective was to determine whether vulnerability of the biological compartment of ecosystems was a function of its exposure to climate change (high physical and chemical vulnerability, Figure 0.8) or depended on other parameters. The main challenge was to quantify system vulnerability to climate change across systems in the first place, then to identify independent variables that could potentially explain it.

The manuscript is organised around 7 chapters as follows:

1) **Chapter 1: Review of concepts.** I define the notion of drivers, give details on our strategy, and present our tools (zoom on palaeo-ecology and dating methods).
2) **Chapter 2: Introduction to the study sites and sediment materials.** Twelve lakes were studied in total. Two lakes, Lake Geneva (FR, CH) and Lake Varese (IT) were investigated extensively, and were used to carry out a meta-analysis. Methodological aspects and un-compiled data (i.e. dating, biological profiles) are presented. In the following chapters, I focus on the ecological processes and concepts that could be derived from our data.
3) **Chapter 3: Summary of the investigation regarding statistical tools.** Across the following chapters, we relied on similar statistical tools i.e. ordination method and additive models to investigate our questions. In this chapter, I introduce these methods, provide a first compilation of the different lake trajectories, and detail some approaches that we will touch on in the remaining chapters.
4) **Chapter 4: Seeking alternative stable states in a deep lake (paper #1, accepted).** We investigated the ecological dynamics of Lake Varese over the past 170 years, and tested the possibility for alternative stable states.

5) **Chapter 5: Ecological vulnerability of Lake Geneva in the Anthropocene (paper #2, under review).** The quantification of ecosystems resilience to climate change is hampered by the simultaneous impacts of multiple stressors. Palaeolimnology allows studying long-term ecological responses of a single system for different levels of local human impact. We reconstructed the ecological state of Lake Geneva over 1,450 years using plankton sub-fossils and questioned whether lake ecological vulnerability to climate variability increased over the course of the past century.
6) **Chapter 6: Drivers of ecological vulnerability to climate across systems (paper #3, in preparation).** We tested whether local human impact is increasing lake vulnerability to climate change by comparing the ecological trajectory of twelve peri-alpine lakes over the last century.
7) **Chapter 7: Discussion.** I discuss the different results and how they may question our vision of ecosystem management.

The last section offers a conclusion on the work carried out in this thesis.

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# Chapter | 1

# General context and strategy

# 1 | GENERAL CONTEXT AND STRATEGY

## 1.1 | SYSTEM DRIVERS

The worldwide spread of anthropogenic local impacts on the environment, as well as their consequences at the global scale, characterize the so-called Anthropocene (Steffen *et al.*, 2011). These human impacts act ubiquitously, simultaneously, and potentially interact between each other both at the global and regional scales. This situation seriously hampers our ability to disentangle the role of climate change from other more locally 'manageable' human impacts such as eutrophication of inland waters for instance. In here, I define the notion of driver, and I present the two main drivers for which the impact on lakes will be quantified *i.e.* climate and eutrophication, as well as their possible interactions.

### 1.1.1 | DEFINITIONS: TEMPORAL ECOLOGY AND DISTINCTION BETWEEN STATIONARY AND NON-STATIONARY FORCING

The terms 'forcing', 'driver', and 'stressor' refers to non-cyclical and/or abrupt, and often non-stationary patterns (Wolkovich *et al.*, 2014), and are used indifferently in the literature to explain ecosystem evolution. Since the early conceptions of Ecology by the Greek philosophers, the field has focussed on spatial aspects of drivers. From the 18th century on, the conceptualization of ecological gradients, food chains, and productivity further justified the spatial approach (e.g. Vadeboncoeur *et al.*, 2008; Horváth *et al.*, 2014). Recently, the development of models and the exponential increase of computing power allowed developing complex multidisciplinary models.

Yet, drivers have both a spatial and a temporal aspect. In fact, other fields of Earth and Natural Sciences have taken in account both dimensions for a long-time (e.g. Darwin, 1859). Wolkowich *et al.* (2014) argue that climate changes introduce into most systems a high-level of temporal variability, that can no longer be left aside from ecosystem modelling. Climate change is characterized meteorologically by atmospheric warming and an increase in the frequency and intensity of extreme events (Meyer *et al.*, 2014). More effort must be put in studying how time may interact with ecological models. It also represents an exciting perspective as some ecological concepts arisen from spatial ecology find echoes in temporal ecology. For instance, nestedness has emerged in community ecology to describe the ordered loss of species along environmental or ecological gradients (Ulrich & Almeida-Neto, 2012). In a nested pattern, the species composition of small assemblages is a nested subset of the species composition of larger ones (Ulrich, Almeida-Neto & Gotelli, 2009). As a result, differences in species richness (and/or species incidence) are a necessary condition for nestedness (Ulrich *et al.*, 2009). The more popular metric to quantify nestedness is the 'temperature' metric, which principle is shown in Figure 1.1. It is based on a presence/absence matrix where rows and columns are ordered in such a way that species (in column) with many occurrences are found in the top-left corner of the matrix and conversely rare species are found in the bottom-right one. Similarly, sites (in row) with high species richness are found in the top-rows, while sites with low species richness are found in the bottom ones. Then, a 'temperature' is calculated for the matrix, according to the predictability of the distribution. The 'temperature' ranges from 0° (highly nested community) to 100° (fully unnested community), as an analogy with water state evolution from solid to gas. The predictability from one community to the other is high whenever the extinction or colonization of species follows the rule that one small community is a subset of any given larger community. In such a case, the temperature is low. Vice versa, the predictability is low for high temperature of nestedness. In natural environment, species may follow a nested pattern along environmental gradient (e.g. Baldi, 2003). Recently, changes in the temporal nestedness of lake algae and zoobenthos communities were detected from palaeo-sequences before critical transitions (Doncaster *et al.*, 2016). The authors compared the nestedness metric evolution to Hill's diversity metric to evidence changes in keystone, weed and canary species before critical transitions. This is only one example where concepts developed in spatial ecology find echoes in temporal ecology but many other ones may be found in the upcoming decades.

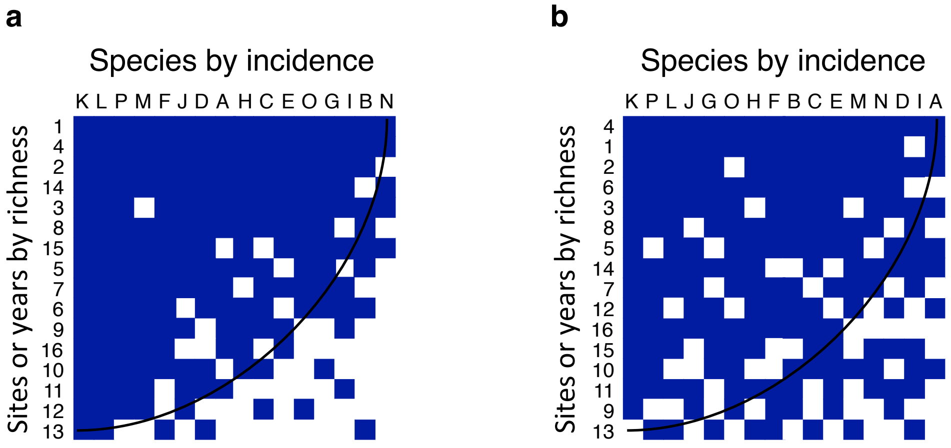


**Figure 1.1 I** Schematic of two incidence matrices sorted by richness and incidence.

(a) High nestedness where sites (row) with low species richness are almost always a subset of sites with high species richness. (b) Unnested community. The temperature is lower for (a) than for (b). The environmental gradient can be either spatial (e.g. Baldi, 2003) or temporal (e.g. Doncaster *et al.*, 2016).

Of course, there are already some long-term ecological research (LTER) sites that have monitored ecosystem responses for decades (e.g. Silvertown *et al.*, 2006). But depending on the system and period of observation, what looks like a linear increase could in fact be part of a totally different dynamics (Figure 1.2). Moreover, another difficulty with temporal ecology lies in the temporal scaling (Wolkovich *et al.*, 2014). Indeed, any observational dataset is characterized by the sampling temporal frequency, the sample period duration, and the event magnitude or departure from previous samples. Events may not be detected or perceived as events if any of these three features is insufficient.

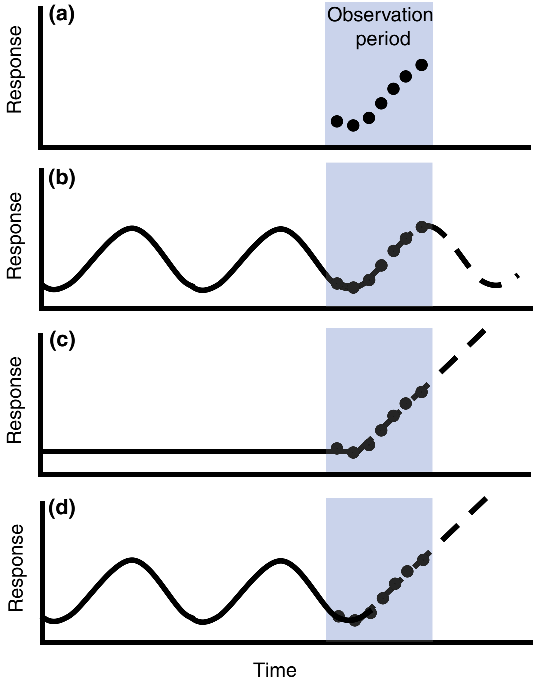


**Figure 1.2 I** Temporal scaling of obserbational datasets.

Long-term records in ecology such as repeated measures or observational data spanning at least 5–10 years are increasingly common. Such data provide an opportunity to improve our understanding and predictive capabilities, but also present a challenge regarding how best to interpret trends. Depending on the system and period of observation, what looks like a linear increase (a) could be part of a regular long-term cycle (b), indicative of a major shift in the system into a non-stationary period (c) or possibly part of both (d), especially if forcing on the system has changed – as seen in many systems with climate change. Temporal scaling and non-stationarity are, thus, inherently linked as any system or process can look stationary or non-stationary depending on the scale. Source: Wolkowich *et al.* (2014).

Figure 1.3 (a) illustrates a final aspect: the stationarity (or non-stationarity, Figure 1.3 b) of the driver. In short, there are two types of drivers. The stationary ones are defined by an underlying probability distribution *i.e.* despite the potential variability, it is possible the minimum and maximum values can be predicted over time. Consequently, an adapted sampling grain (interval) and extent (duration) allows collecting information on both response and recovery of systems to forcings.

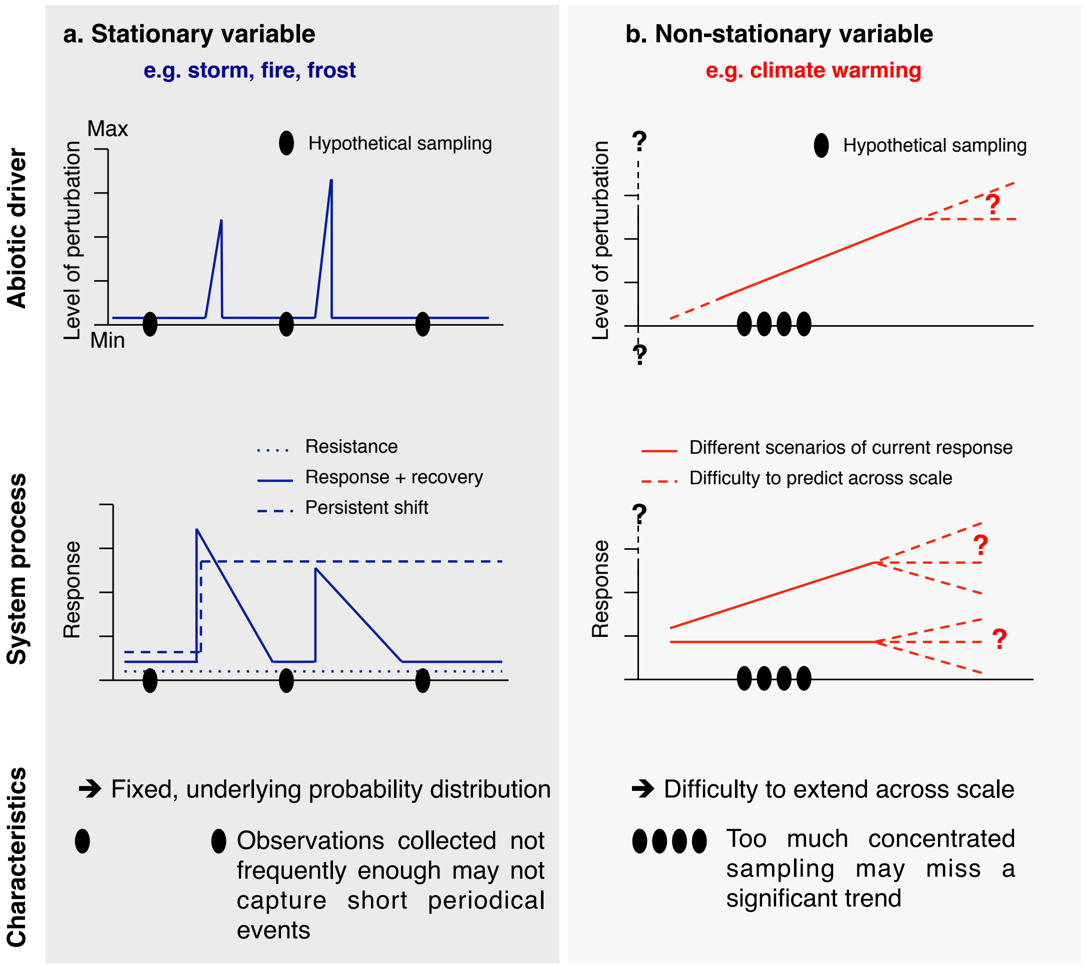


**Figure 1.3 I** Classifications of events in two groups according to Wolkovich *et al.* (2014).

Stationary variables (a) have a fixed underlying probability distribution. They can be cyclical or extreme events. On the other hand, non-stationary variables (b) may cause a sudden shift in the ecosystem, and linear interpolation from short-time scale interpolations is rarely confirmed by observations (Schnute & Richards, 2001). Sampling resolutions will also impact the way we apprehend both types of forcing *i.e.* a sparse sampling may miss extreme events while a high-frequency sampling over 2 years won't be enough to identify with confidence any non-stationary trend.

For instance, extreme events (e.g. storms, fires, frosts, droughts), despite the inherent stress they cause on ecosystems, are stationary variables. Indeed, the distributions of storms can be apprehended from high-frequency monitoring programs, and it is possible to set minimum and maximum values that will encompass the distribution of the majorities of events (e.g. the daily precipitations in the high-altitude catchment of Lake Varese ranges from 0 to 80 mm.day$^{-1}$ during summer, Figure 1.4). The impacts can be highly variable e.g. storms will have small or big impact on the lake (Perga *et al.*, Under Review), but these modifications are transient in most cases. In other words, while the frequency of such extreme events is expected to increase with climate change (Meyer *et al.*, 2014), the distribution maximum and minimum are stationary (Figure 1.5 a).

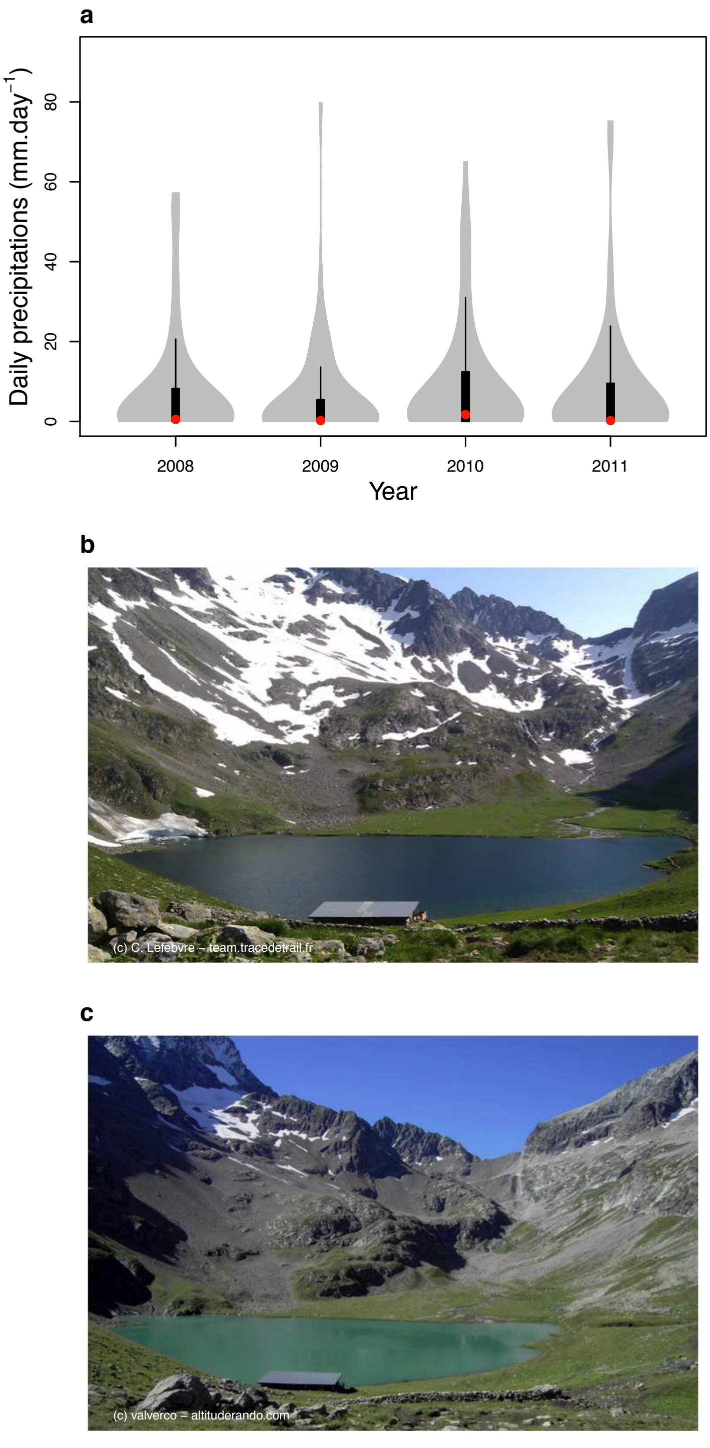


**Figure 1.4 I** Example of a transient response (turbid state) to a discrete forcing (storm) in Lake Muzelle (Fr) (Perga *et al.*, Under Review).

Storms are characterized as extreme events, but they follow a known probability distribution (e.g. 2 to 5 storms per summer). (a) Violin plots showing the probability density, median and interquartile range of summer precipitations (July, August) from 2008 to 2011. High-frequency monitoring reveals the daily distribution of precipitations in high-altitude catchment of Lake Varese (Fr). More than 40 mm.day$^{-1}$ of precipitations is rare. Storm impact on the high-altitude lake depends on the watershed state (see Perga *et al.*, Under Review), and the effects are transient, despite a wide range of recovery time. Lake Muzelle before (b) and after (c) a storm.

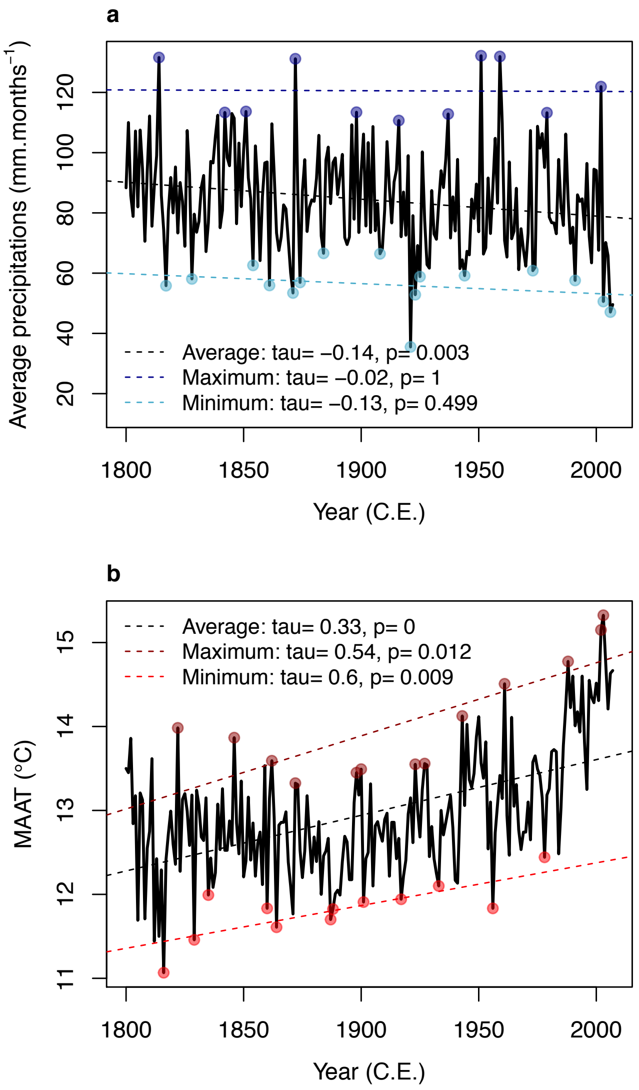


**Figure 1.5 I** Precipitations and air temperature evolution in Milano (IT) for the 1880-2007 period (HISTALP dataset, Auer *et al.*, 2007).

Dots represent years with maximum and minimum values over rolling windows of 30 years (a) The mean precipitations are decreasing, but the maximum and minimum precipitations over 30 years are stationary. (b) Mean annual air temperature (MAAT) is increasing over the period, as well as the minimum and maximum.

On the other hand, atmospheric temperature is a non-stationary variable over large time-scale (Figure 1.5 b). As a consequence, any response observed at a specific time may not be extrapolated linearly in the future (Figure 1.3 b). This persistent forcing may have persistent impacts (e.g. lakes surface temperature correlated to climate warming over the years, Woolway *et al.*, 2017), or transient ones (e.g. regime shift between green to desert Sahara, Figure 1.6).

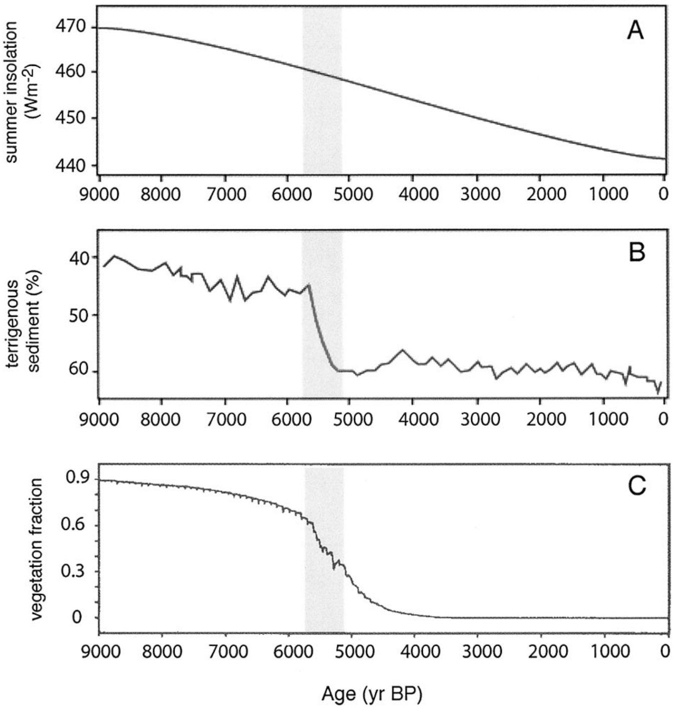


**Figure 1.6 I** Example of a persistent transient to a non-stationary continuous driver: regime shift from vegetated to desert state in Sahara (redrawn by Foley *et al.*, 2003).

Incoming solar radiation in summertime (a), abrupt change in the climate and vegetation cover over the Sahara roughly 5500 years ago (b), simple coupled atmosphere–ocean–vegetation model demonstrating how a switch from a green Sahara to a desert Sahara could occur (c), even with the model only forced by slow changes in incoming solar radiation (a). A and B were redrawn from deMenocal *et al.* (2000) C was redrawn from Claussen *et al.* (1999).

To sum up, precise definition of which types of temporal events are being addressed is still under-looked while it could really benefit the field to (1) acknowledge the temporal aspect of forcing and (2) have a better classification of events (stationary and non-stationary). We embrace the definition given by Wolkowich *et al.* (2014): forcing events may be discrete (e.g. a fire or drought) or persistent (e.g. long-term warming trends). The ecological response may be transient (temporary, e.g. a plant down-regulating initial photosynthetic enhancement in response to elevated CO2 concentrations, Leakey *et al.*, 2012) or persistent (continuous). Our view differ from the one of Wolkowich *et al.* (2014), as we hypothesis that there could also be a state of non-response *i.e.* resistance (Figure 1.7).

Why are these definitions specifically relevant to us? Quantifying ecosystems resilience is a real challenge for the 21st century ecologists. Yet, we found actually few examples of resilience studies for non-stationary, persistent forcings, such as climate warming. In fact, most evidences have been gathered for stationary components of climate change (mainly extreme events e.g. floods, fires, droughts). This is probably due to lack of observational datasets. On the other hand, even long-term resilience working groups (Cole, Bhagwat & Willis, 2014) will often focus on fires event to measure recovery. It is greatly relevant to do so, and there are many questions that can be answered with such approach, including the quantification of recovery capacity of ecosystems. However, in order to predict the ecosystem resilience capacity to climate warming, atmospheric warming is the forcing to be studied.

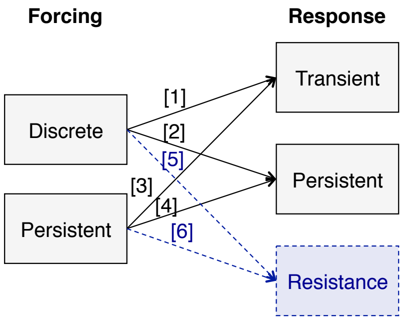


**Figure 1.7 I** Classification of events and responses.

Wolkowich *et al.* (2014) argue that an improved classification of events could improve the understanding of the role of events in shaping ecological systems. In particular, ecosystem responses to discrete events (e.g. frost, droughts) may be either short lived and transient [1], or persistent and continuous, reflecting changes in the background state (e.g. climate change, introduction of invasive species, habitat fragmentation) [2]. Similarly, however, persistent forces may give rise to transient ecological responses [3] or persistent responses [4]. We further hypothesize that both discrete and persistent forcing may drive no response in natural ecosystem in which case they exhibit resistance [5, 6]. Modified from Wolkowich *et al.* (2014).

### 1.1.2 | CLIMATE

While climatic fluctuations have coerced the prosperity and demise of past human societies over centuries (Büntgen *et al.*, 2011; Zhang *et al.*, 2011; Tallavaara *et al.*, 2015), humans themselves have now become a major driver in climate evolution since the 19th century (Rosa & Dietz, 2012) (Figure 1.8).

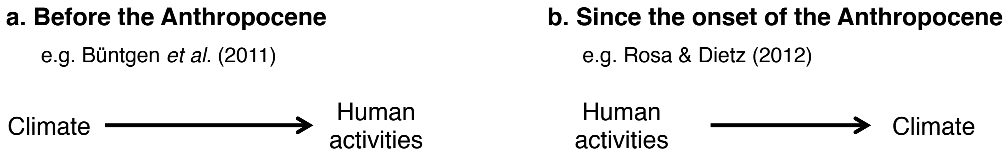


**Figure 1.8 I** Conceptual relationship between climate and human activities.

Before the Anthropocene (a), climate was driving populations prosperity and collapse while for the past century at least, human activities have been driving climate (b).

Most ecological processes, terrestrial, freshwater and marine ecosystems included, show responses to anthropogenic climate change (Scheffers *et al.*, 2016). They range from the genetic (Geerts *et al.*, 2015) to the phenological scale (shift in time) and species modifying their geographic (shift in space) distribution (Parmesan & Yohe, 2003). As a response to climate change, species can be also shrinking in size (Sheridan & Bickford, 2011), and modifying their physiology (Chown *et al.*, 2010). These changes affect food webs and result in new interactions (change in vertical biodiversity). Disruptions scale from the gene to the ecosystem have documented consequences for people, including unpredictable fisheries and crop yields, loss of genetic diversity in wild crop varieties, and increasing impacts of pests and diseases (reviewed in Scheffers *et al.*, 2016).

Independently from the recent warming documented through monitoring, air temperature reconstructions support large climate fluctuations during the Holocene. The past 1500 years were notably marked by a cold period starting with a volcanic eruption (Larsen *et al.*, 2008), which lasted longer than previously thought (Dark Age, 536 – 660 AD) (Büntgen *et al.*, 2016), followed by a prolonged period with both minimal explosive volcanic activity, and no significant perturbations in solar forcing, either positive or negative (Medieval Quiet Period, ~725 – 1025 AD) (Bradley, Wanner & Diaz, 2016), then by successively a warmer period (Medieval Warm Period MWP, 900 – 1400 AD) (Pfister *et al.*, 1998; Bard *et al.*, 2000; Guiot, Corona & ESCARSEL members, 2010), another cold period (Little Ice Age LIA, 1500 – 1800 AD) (Luterbacher *et al.*, 2004; Ljungqvist, 2010), and the recent warming (recent Climate Change rCC, 1970 – present). Critics argued that the presence of this natural oscillation between warm and cold period provides evidence of the natural aspect of rCC. However, the argument suffers from the vague definition of the period to which MWP refers to (Bradley *et al.*, 2016). There are actually significant time offsets in warming in different regions (Crowley & Lowery, 2000). Ignoring them can lead to serious errors when inferring of Medieval warmth magnitude and its relevance to the late 20th century warming interpretation. Moreover, failure to substantiate hemispheric warmth greater than the present consistently occurs in composite reconstruction when not accounting for time offsets (Crowley & Lowery, 2000). It is thus essential to choose a relevant reconstruction of the climatic forcing, but also identify the region it accounts for, as some signals are more regional than others. For the past 1500-years period, several climatic components have been reconstructed. Summer temperatures have been classically reconstructed using dendrochronological approaches (Büntgen *et al.*, 2006, 2011) or stalagmite isotopic composition (Mangini, Spötl & Verdes, 2005), and winter temperatures from documentary data (Pfister *et al.*, 1998). Hydrological events frequency has been approached by tree-ring based reconstruction of debris flows (Stoffel *et al.*, 2008) or biogeochemical signature of sediments (Wilhelm *et al.*, 2012, 2013), solar irradiance by a cosmogenic nuclides based approach (Bard *et al.*, 2000), and insolation quantities by modelling orbital solution including general relativity and lunar influence impacts (Laskar *et al.*, 2004). The reconstructed signals can then be tested against each other, or compared with glacier dynamics described elsewhere (Joerin, Stocker & Schlüchter, 2006).

As a consequence, the MWP defined as the 900 – 1400 AD period by Bard *et al.* (2000) is restricted to a period with less severe winters from 900 to 1300 AD by Pfister *et al.* (1998). Guiot *et al.* (2010) who studied the signal at the European scale identify a start as early as 800 AD and a end in 1250 as a cooling appeared over the European south-west and extended progressively to entire continent by 1400 AD. This period is coherent with a warmer period from 800 to 1300 AD reconstructed for altitude systems in the Alps (Mangini *et al.*, 2005), and extra-tropical Northern hemisphere (Ljungqvist, 2010). However, Casty et al. (2005) reports warm summer around 1550 AD, a period that many studies would place in the LIA (Ljungqvist, 2010). Overall, the centring is not systematically coherent, and the impact on systems is sometimes cryptic. Modelling approaches can bring further understanding on how system responses to various forcings are tightly linked. For instance, during the Holocene, the Rhone Glacier expansion was primarily temperature-driven via changes in summer insolation (Goehring *et al.*, 2012). Other climate simulations reveal results less straightforward than previously assumed, such as the 1000-years long cooling trend of sea surface temperatures (SST) for the pre-industrial Common Era induced by a net negative radiative forcing resulting from repeated clusters clouds of volcanic eruptions (McGregor *et al.*, 2015). At the other end of the spectra, palaeolimnologic reconstruction in small lakes support the occurrence of MWP and LIA (Morellón *et al.*, 2011).

In order to assess the impact of climate change on lakes trajectories, we used long-term weather records as a climatic forcing for the past century (Auer *et al.*, 2007), and long-term reconstruction (755-2004) to cover the past millennia (Büntgen *et al.*, 2006).

### 1.1.3 | EUTROPHICATION

Despite being an important threat to freshwater and marine ecosystems throughout the world (Smith, 2003), eutrophication is a local forcing. As a consequence, the lakes of our study (and in general) show several levels of eutrophication. Their sediments are natural archives of past environmental changes and represent the only way to assess the impact of human activities on lakes for the period preceding the onset of monitoring programs or first surveys (Figure 1.9). With the premise of covering a long-enough period, they make possible to establish reference conditions (Smol *et al.*, 2001; Battarbee *et al.*, 2005; Dubois *et al.*, 2017). While in some cases the history of eutrophication ranges over several centuries (e.g. Hernández-Almeida *et al.*, 2017), water enrichment has been a relatively recent phenomenon taking place over the past 100 years in most large lakes such as those in the peri-alpine area (Tolotti *et al.*, In revision; Capo *et al.*, 2016; Milan *et al.*, 2017). While we hypothesise that low local human impact (Figure 1.9 a) had little impact on lakes trajectories before the large development of cities (Figure 1.9 b), we used a palaeolimnological approach to determine the start of enrichment for as many sites as possible (Battarbee *et al.*, 2005).

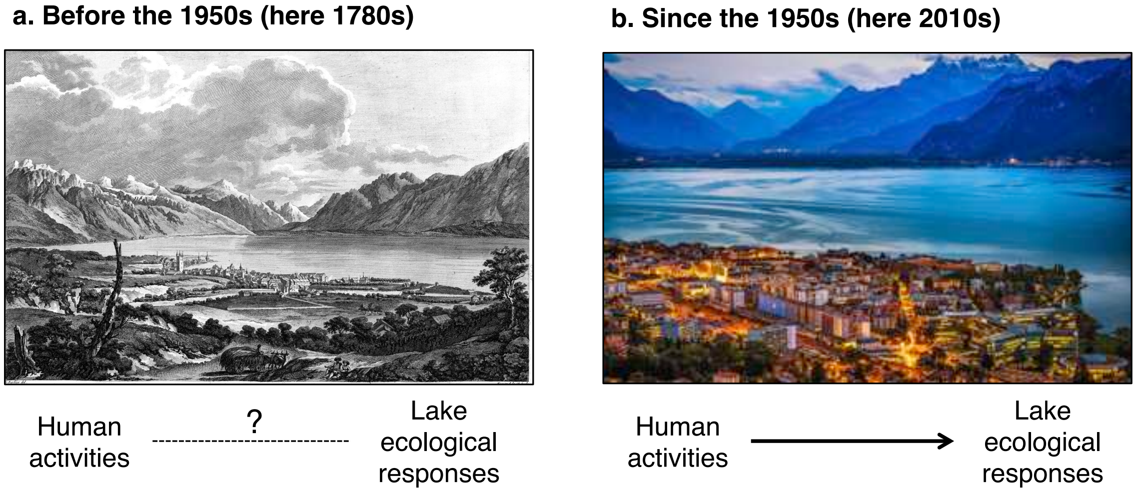


**Figure 1.9 I** View on Lake Geneva from Vevey (CH) **(a)** in the 1780s © VIATICALPES and **(b)** in the 2010s © Reflectim.
The human impact on lake ecology before the onset of the monitoring program (1957 for Lake Geneva) is unknown without resorting to palaeolimnology, but abundant data is available since the 1950s (e.g. Anneville *et al.*, 2009; Perga *et al.*, 2015).

### 1.1.4 | INTERACTION BETWEEN DRIVERS

Most ecosystems are submitted to several simultaneous stressors. This ‘allied attack’ (Moss *et al.*, 2011) greatly restricts our corridor of action, while it also provides hope for manager to reduce the risk arising from global change by reducing local stressors (Scheffer *et al.*, 2015; Rocha *et al.*, 2015). This assertion should be re-evaluated depending on stressor interaction mechanism. Some stresses simply do not interact one with the other. Their combined effect is said to be additive, which is the sum of their individual effects. When stresses do interact with one another, their combined effect can be greater than the additive expectation, *i.e.* the two stresses act in synergy. If the combined effect is less than the additive expectation, the two stresses are antagonistic. In fact, the summary presented in Figure 1.10 is more accurate if the magnitude and direction of the cumulative effect and interaction effect in absolute terms are also interpreted (see Piggott *et al.*, 2015). Besides, the picture is made more complex by the fact that different interactions can act at different levels of ecological organisation (Brown *et al.*, 2013; Piggott *et al.*, 2015).

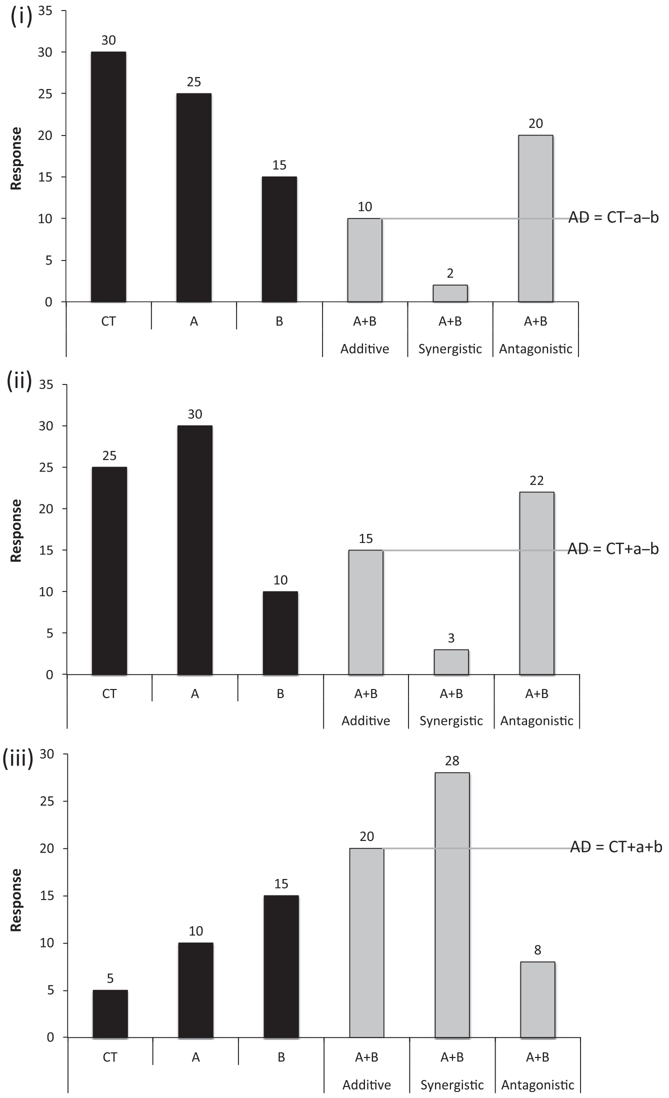
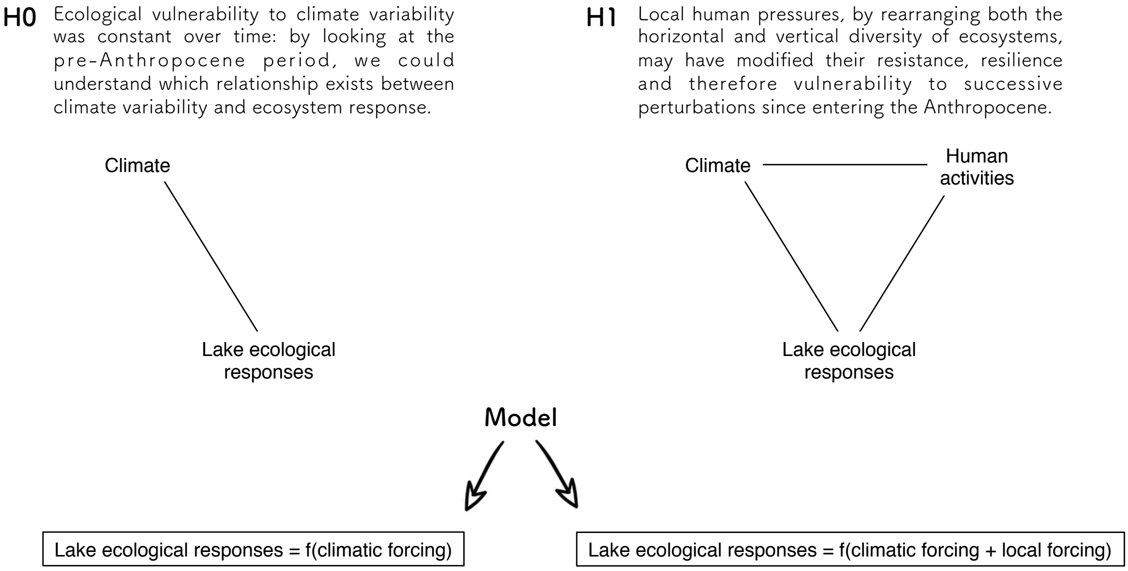


**Figure 1.10 |** Conceptual approach to interpreting interaction types from response data presented in factorial studies.

Treatments in factorial studies include control (CT), with stressor A (A), with stressor B (B), and with both stressors (A + B). Interaction types are classified as additive, synergistic, and antagonistic, depending on the A + B response compared to the additive sum (AD) of individual effects for stressor A (a), B (b) relative to the control (CT). The three plots show interaction types that have double-negative (i), opposing (ii), and double-positive (iii) individual stressor effects on the response variable of interest. Redrawn by Piggot *et al.* (2015) from Crain *et al.* (2008).

In our case, climate change and eutrophication have largely been shown to have similar impact on lakes (reviewed in Moss *et al.*, 2011), including anoxia (Jenny *et al.*, 2016), cyanobacteria growth (Kosten *et al.*, 2012), and average smaller size of *Daphnia* spp. (Gillooly & Dodson, 2000).

Because of these interactions between several stressors, it is often difficult to know which changes in the community composition are solely due to climate variability. Palaeolimnology has been seen as an interesting way to study ecosystems trajectories under lower human impact (e.g. Capo *et al.*, 2016). Yet, this approach neglects the possible interactions between stressors, and considers that climate change and eutrophication have an additive effect. In such cases, we assume that ecological vulnerability to climate variability is constant over time (Figure 1.11, H0). As a result, by looking at the pre-Anthropocene period, we can understand the relationship between climate variability and ecosystem response. However, as only roughly 1 out of 4 interactions are additives (Piggott *et al.*, 2015), it may have changed due to the addition of a new stress *i.e.* local human impact (Figure 1.11, H1).



**H0** Ecological vulnerability to climate variability was constant over time: by looking at the pre-Anthropocene period, we could understand which relationship exists between climate variability and ecosystem response.

**H1** Local human pressures, by rearranging both the horizontal and vertical diversity of ecosystems, may have modified their resistance, resilience and therefore vulnerability to successive perturbations since entering the Anthropocene.

**Figure 1.11 I** Two working hypotheses for ecosystem responses to climate variability.

H0 assumes there are no interactions between global and local forcings. As a consequence, we can analyse the impact of climate variability on lake ecological responses by looking into the past for periods with lower human impact. H1 supposes that the addition of human activities to the equation may have modified lake ecological responses to climatic variability.

## 1.2 | RESILIENCE AND ITS QUANTIFICATION

Building ecosystem resilience, the ability of a system to withstand external stresses and disturbances (Gallopín, 2006), is one of the major guidelines stated by the UNEP roadmap to maintain ecosystem functions and services (Epple & Dunning, 2014). Resilience is expressed either by the ability of a system to resist change when faced with a disturbance (resistance) or to return to a stable state following disturbance (recovery) (Hodgson *et al.*, 2015). Resilience is theoretically tied to ecosystem diversity (Walker, Kinzig & Langridge, 1999; Elmqvist *et al.*, 2003). Indeed, a more diverse community (horizontal diversity) is more likely to host a larger panel of responses to environmental change, thereby increasing the probability of persistence and recovery after a disturbance. High recovery is more likely in ecosystems that include cross-scale redundancy *i.e.* member of a same functional group operating at different space scales (Nash *et al.*, 2016). Furthermore, the patchy distribution of species in heterogeneous habitats would desynchronize climatic-driven fluctuations in populations (Holling, 1973; Loreau, Mouquet & Gonzalez, 2003; Virah-Sawmy, Gillson & Willis, Katherine J., 2009). In addition, a reduction in horizontal diversity would trigger an extinction cascade, *i.e.*, a loss of vertical diversity (Srivastava & Bell, 2009).

As more and more management plans will require ecosystem resilience quantification, resilience measurement methodology deserves academic attention. In this section, I first discuss the conceptual implications of resistance and recovery. Then, I present an overview of the tools we used to quantify responses in the following chapters.

### 1.2.1 | RESISTANCE, RECOVERY: BASIN OF ATTRACTION OF ECOSYSTEMS

Resistance and recovery are illustrated by the much used and helpful image of the basin of attraction, often depicted as a ball in a valley under the action of gravity (Carpenter, 2005; Scheffer *et al.*, 2009). The idea is based on the premise that an ecosystem exists in a stable state (Figure 1.12 a). Internal feedback makes the ecosystem resilient to external drivers. This means that even if the ecosystem responds to the driver (disturbances), it will eventually come back to the center of its basin of attraction *i.e.* its stable state (Figure 1.12 b to d) when the disturbance is off. In shallow lakes for instance, internal feedbacks include presence of macrophytes that may stabilize the sediments (Ibelings *et al.*, 2007), clean the water from its nutriment, and provide habitat for large plankton grazers that contribute to algae growth regulation (Gianuca, Pantel & Meester, 2016). An underlying implication of feedback presence and their strength is the variability of the ecosystem state. Indeed, an ecosystem with strong feedback mechanisms will recover very rapidly from a disturbance (or alternatively resist to this disturbance), so the range of variation will be narrow (Figure 1.12 e). If the feedback mechanisms are weak or non-existent, the range of variation will be broad in the ecosystem state will be high (Figure 1.12 f).

The basin of attraction concept has powerful explanatory power in ecosystem management. Indeed, it is possible to infer that if internal feedback mechanisms are gradually lost because of driver increase (and thereby the valley morphology gets flatter), then the variance will gradually increase, providing an early warning signal (EWS) of the ecosystem degradation (Carpenter & Brock, 2006). Variance is a readily metric, easily computed from monitoring data (as long as the sampling resolution is relevant to the process). As a result, it has often been adopted as a valuable metric of resilience loss, and as an indicator of the ecosystem getting close to a catastrophic transition (Carpenter & Brock, 2006).

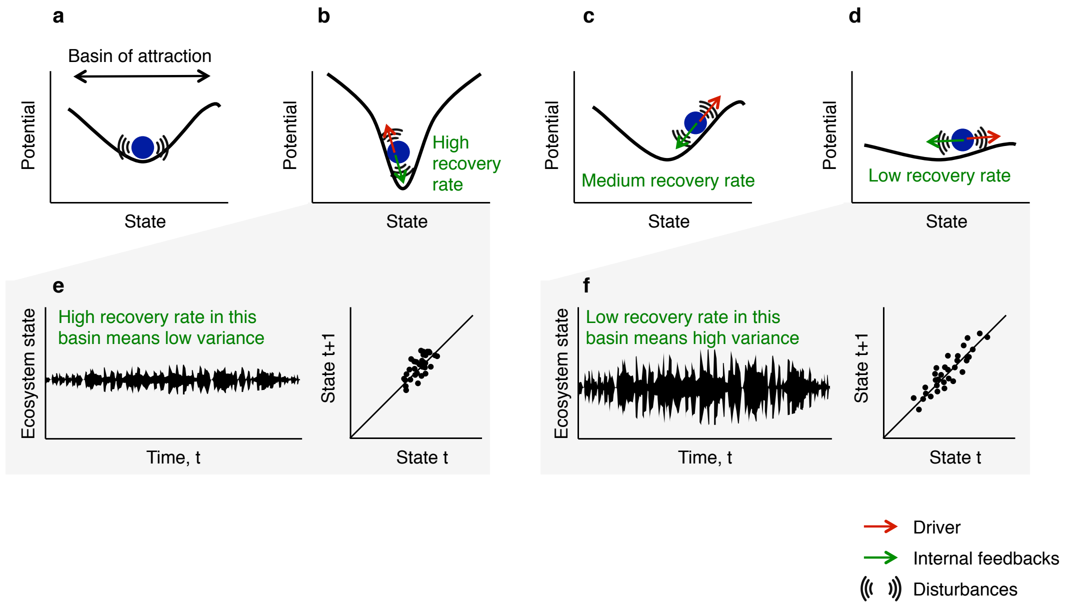


**Figure 1.12 I** Concept of stable state adapted from Scheffer *et al.* (2009).

(a) The ball (blue circle) in the valley symbolises the ecosystem in its basin of attraction. A change in driver may push away the ecosystem from the centre of its basin of attraction (b, c, d). Depending on the strength of the internal feedback, the ecosystem may deviate more or less from its equilibrium (explicit gradient from (b) important internal feedback and high recovery rate to (d) *i.e.* low internal feedback and low recovery rate. Note that instead of recovery, we could also consider that the difficulty to move the ball means that the system is highly resistant. When recovery or resistance is high (or when no driver is pushing the ecosystem away from the centre of its attraction basin), one observation to the other will be very similar and the variance is low (e). On the contrary, an ecosystem with low recovery rate or low resistance displays high variability and high variance (f).

Besides ecosystems degradation, it is possible that beyond a certain threshold, or tipping-point (van Nes *et al.*, 2016), the ecosystem may not have time to recover or just be too far from its basin of attraction (Figure 1.13). Then, any additional forcing may cause the system to shift in an alternative stable state, where new internal feedback mechanisms will operate (consequently, the variance becomes low again, Figure 1.12 e). Even if the perturbation decreases below the initial threshold, the ecosystem may remain in the new state, as an hysteresis loop is formed. This defines ‘regime shift’, or critical transitions *i.e.* large, non-linear, persistent changes in the structure and function of a system (Scheffer *et al.*, 2001; Scheffer & van Nes, 2007).

Finding early warning signals (EWS) of such transitions is understandably gathering a lot of efforts in the scientific community, as demonstrated by the amount of literature dealing with the subject (Carpenter & Brock, 2006; Scheffer *et al.*, 2009; Carpenter *et al.*, 2011). Yet, warnings are issued against catastrophic transitions that may occur without EWS (Brock &

Carpenter, 2010; Dakos *et al.*, 2015; Burthe *et al.*, 2015), or regime shifts that occur without any early warnings (Hastings & Wysham, 2010), or additionally the presence of variance in the system that will not be followed by any catastrophic transition (Spears *et al.*, 2017).

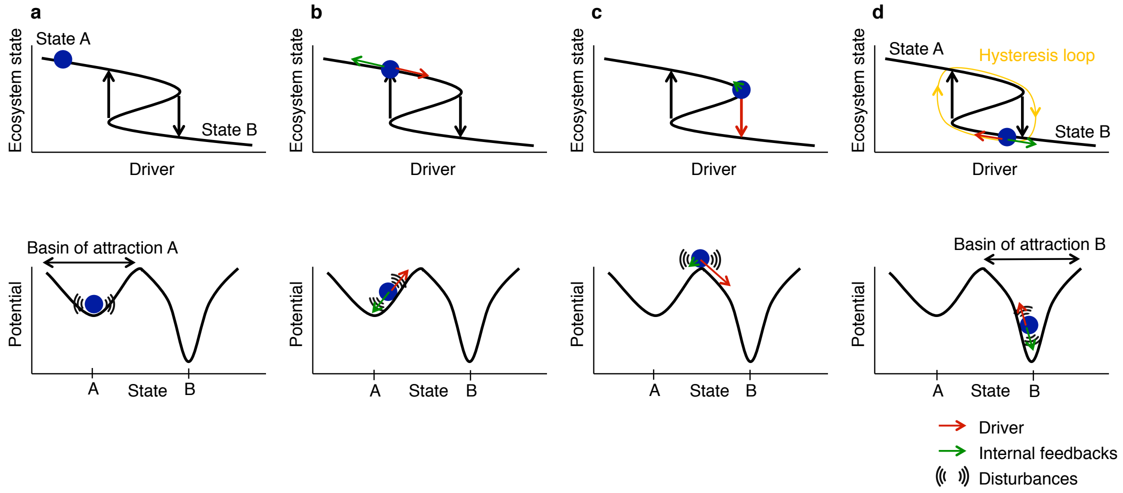


**Figure 1.13 I** System approaching a regime shift with fold catastrophe model (top) and corresponding stability landscapes (bottom).

In its initial state (a, b), a slow change in driver is buffered by the system that remains in its initial state. However, above a certain threshold (c), only a small forcing may be able to push the ecosystem towards an alternative stable state (d). In this new state, even if the driver returns below the threshold level, the ecosystem will remain in the alternative stable state.

### 1.2.2 | QUANTITATIVE ECOLOGY

There are several tools available to quantify ecosystems evolution. Herein, we often relied on general additive models (GAM) that are well adapted to a single-variable response to multiple drivers (Simpson & Anderson, 2009; Wood, 2016). The identification of the driver for a given transition is mandatory to characterize its threshold process (Andersen *et al.*, 2009). Additive models are a nonparametric form of regression where the relationship between response and explanatory variables is derived directly from the data (Simpson & Anderson, 2009), rather than being assigned a prescribed functional form (e.g., linear or quadratic). Local relationship between response and covariates can be modelled through this approach, which is more realistic as, at least for lakes, most of them are non-linear (Frossard, Rimet & Perga, 2018). Moreover, GAM are able to resolve the issue linked with uneven sampling, an inherent issue of palaeo-ecology, by including correlation structure in the model (autoregressive AR(1) or continuous autoregressive CAR(1)).

However, GAM does not account for non-linear vulnerability to a driver, which theoretically happens if a system undergoes a regime shift, or alternatively, if it loses resilience to a given forcing due to multi-stressor interactions. This gap opens interesting perspective in developing a model that could account for a change in vulnerability; in the meantime, the method exposed in Chapters 3 and 5 can be reused. Operationally, we summarized the variability in the ecological assemblage into ordination axes. Then, we detected the major transitions resorting to the change point analysis (Killick *et al.*, 2016); we split the record in two, the first gathering the points up to the threshold, the second the points beyond it. Finally, repeating the on each and every window before and after the identified transitions to see if the estimations hold will strengthen the results.

Another way of quantifying resilience is to measure its components (resistance and recovery) separately. This approach requires defining a reference state. Consequently, the amplitude of changes from the baseline quantifies the resistance of the system, while the

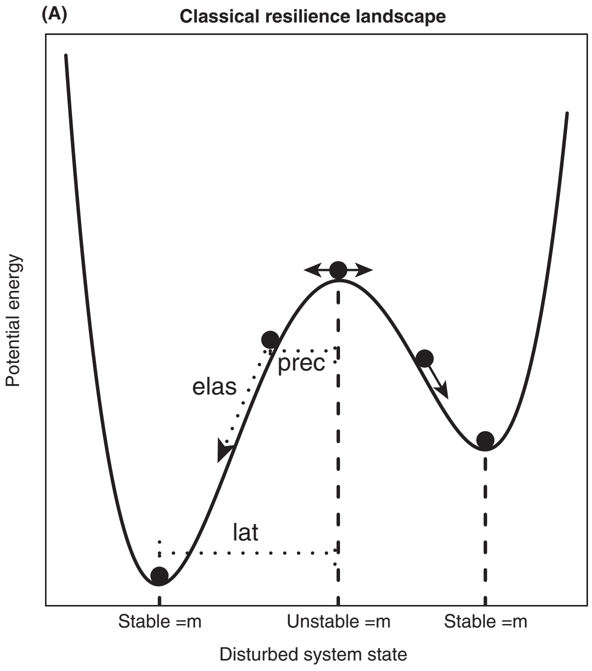


**Figure 1.14 I** Resilience landscape, and different component of resilience according to Hodgson *et al.* (2015).

Tipping points, representing unstable equilibrium states, are the peaks of the landscape. Each stable equilibrium (=m) has ‘latitude’ (lat: distance in state to the nearest tipping point), and each disturbed state has ‘precariousness’ (prec: distance in state to the nearest tipping point), and ‘elasticity’ (elas: rate of return to the local attractor equilibrium).

required time to go back to its previous state defines its recovery (Figure 1.14). In Chapter 5, we only address the resistance component. Indeed, as climate warming is a non-stationary forcing that displays a monotonic trend (Figure 1.3), we are unable to provide any estimate of the system recovery capacity.

Lastly, measuring EWS of change can inform on potential type of transition (e.g. did the system undergo a regime shift? Then, can we measure resilience loss? See Figure 1.12). Knowing the limitation of EWS (Dakos *et al.*, 2015; Burthe *et al.*, 2015; Capon *et al.*, 2015), we quantified them for Lake Varese assemblage as we suspected the system underwent a regime shift.

Figure 1.15 present the workflow analysis developed in Chapter 4 to detect regime shift transitions from palaeo-datasets. The first step requires transforming multivariate data into univariate axes that summarise the maximum variability. Change-points are identified along these axes, symbolising the major transitions within the assemblage. Regime shifts are by definition abrupt. In an earlier version, we ran ARIMA models at this step to make the decision, but this can in fact be assessed visually (see Chapter 4). The potential drivers for the transitions were thereafter identified using GAM. Then, the shape of the relationship was evaluated to identify any potential bistability. EWS were computed along that final step to detect any potential loss of resilience in the system.

To sum up, the novelty we are bringing in this work is acknowledging that the well-accepted (yet still worth defining, see Piggott *et al.*, 2015) concepts of additive, synergetic and antagonistic effects of multi-stressors (Folt *et al.*, 1999; Brown *et al.*, 2013; Piggott *et al.*, 2015) find parallel at a temporal perspective. As ecosystems display a 'recovery debt' (*i.e.* the interim period during the recovery process characterized by biodiversity and functions deficit, Moreno-Mateos *et al.*, 2017), we advocate that the legacy of a previous stressor may change the vulnerability of system to climate change, that may persist beyond restoration.

While quantifying resilience is appealing, it was also important to study the qualitative aspects of the transitions. In other words, we always tried to answer 'what are the processes at work for a given transition?' For instance, in Chapter 4, we used both qualitative and quantitative tools. We used additive models with smooth parameters (Simpson & Anderson, 2009; Wood, 2016) to isolate potential drivers contributions (eutrophication and climate change). We also investigated whether EWS occurred before the transition. Along with the quantitative approach, we investigated the abrupt shift explanatory process: we found that the littoral zone was the first one to collapse, possibly unravelling its buffering role in the early stages of eutrophication.

Regime shift detection from palaeo-datasets

| Workflow analysis | Method | Input data | Output |
|---|---|---|---|
| **Ordination** | Ordination methods:<br>- PCA (H1: linearity)<br>- DCA (H1: unimodality) | C | $C_{DCA1}$, $C_{DCA2}$ |
| **Transitions** | Change-points method (AIC computation to determine the significant number of transitions) | $C_{DCA1}$, $C_{DCA2}$ | Transitions on $C_{DCA1}$ and $C_{DCA2}$ |
| **Dynamics** | Exploration: ARIMA model predictions ➔ very trivial so decision eventually made visually | $C_{DCA1}$, $C_{DCA2}$ | Dynamic of the relationship: abrupt vs. linear |
| *Abrupt* *Linear* | | | |
| **Forcing** | GAM **(Modelling approach)** | Response ~ Forcing(s)<br>- Response: $C_{DCA1}$, $C_{DCA2}$<br>- Forcings: I-TP, MAAT (single or combined) | Deciphering contributions of several forcings to lake ecological response |
| **Shape of the relationship** | Plot **(Plotting approach)** | Response ~ Forcing(s)<br>- Response: $C_{DCA1}$<br>- Forcings: Selected forcings (GAM output) | Response vs. forcing relationship |
| *Regime shift* *Step change* | | | |
| **Early warnings** | Mann Kendall test on SD and ACF evolution (raw and residuals);<br>t-test before/after transition. | $C_{DCA1}$ AR(1) and SD<br>$C_{DCA1(residuals)}$ AR(1) and SD | - No trend (or diminution)<br>- Positive trend before transition<br>- Positive trend before transition + diminution after transition |

**Figure 1.15 I** Summary of the workflow analysis developed for regime shift detection from palaeo-datasets (Bruel *et al.*, 2018).

This workflow analysis was applied in Chapter 4. AR(1): autocorrelation, C: Cladoceran assemblage, $C_{DCA1,2}$: Axes 1 & 2 of cladoceran assemblage, GAM: General Additive Models, I-TP: Inferred Total Phosphorus, MAAT: Mean Annual Air Temperature, SD: variance.

## 1.3 | METHODS AND STRATEGY

Through the two first sections of this chapter, we often highlighted how the lack of perspective is detrimental to the field of Ecology, especially when trying to address the impacts of climate change. Ecological monitoring records do not typically extend beyond the past few decades; on the other hand, palaeoecology is key to defining ecosystems pre-anthropogenic variability (Seddon et al., 2014). In this section, I quickly present what I refer to when writing 'palaeolimnology'. Then, I list the different methods used to characterize and date sediment cores. After that, I introduce the main proxies we used to answer our questions. Finally, I present all the study sites within the geographical area of interest.

### 1.3.1 | LONG-TERM ECOLOGICAL TRAJECTORY

The previous sections already hinted toward the importance of long-term perspective when studying climate change. Indeed, as the observation of climate change requires records of 30 years at least to decipher between natural variability and climatic trend (Figure 1.2), most monitoring program do not cover a long enough period. The study of the impacts of climate change on ecosystems should encompass greater periods to rule out significant drivers from non-significant ones.

Palaeolimnology offers the opportunity to cover long period of time before many monitoring programs even started. They offer the possibility to get an objective probability framework for changes observed in ecosystems (Spears *et al.*, 2017). However, there are some inherent challenges in using these data:

- The lake sedimentation rate must be adequate for the investigated questions *i.e.* a too low sedimentation rate makes it impossible to investigate ecological questions. For our purpose, 0.5-2 $cm.yr^{-1}$ is an ideal sedimentation rate, providing enough time resolution without having to sample too long sequences to cover the past century.
- There is a spatial heterogeneity in the sedimentation in the lake due to extreme floods, earthquakes, and 'spontaneous' delta collapses (Kremer *et al.*, 2015a). The sediment cores we selected had to be in regions of the lakes that were far enough from the main inflows to avoid disturbances. Indeed, instantaneous deposits must be removed from the sequence, and in a highly disturbed part of the lake, the risk of forgetting a layer is higher.
- Sediment cores must be sampled, and long, undisturbed records are harder to get.
- Sediment must be dated.
- Indicators have to be inferred *i.e.* TP inferred from diatom assemblage, ecological state from cladoceran assemblages.
- Accurate statistical tools have to be used.

This chapter summarizes the different analytical methods used during the PhD. Then, the study area is briefly presented.

## 1.3.2 | METHODS FOR SEDIMENT CHARACTERISATION AND DATING

### 1.3.2.1 | Dry weight and loss on ignition

Every subsample was characterized beforehand by quantifying its dry weight (DW) and its organic matter (OM) content. The procedure described in Heiri *et al.* (2001) consists in weighing fresh sediment before and after a 48h-stay in an oven at 60°C. Loss on ignition (LOI) analysis was thereafter conducted on the dried sediment (4h-stay in an oven at 550°C), allowing an estimation of the OM content. Finally, carbonate content was measured on some cores (Lake Varese and Lugano samples, see later sections) by weighing the residual mass of the same sediment after a last oven treatment (2h, 950°C).

Standardization by water content ($m_{\text{fresh sediment}} - m_{\text{dry sediment}}$) allowed comparing the abundances in sediment samples used for biological analysis.

#### 1.3.2.2 | Method of radionuclide dating

Measuring radionuclides activity in the sediment can date the past century. Pierre Sabatier and Jean-Louis Reyss undertook most radioelement measurements presented herein on dry sediment samples at the Modane Underground Laboratory (LSM) using well-type germanium detectors.

Since 1955 and for a decade, nuclear weapons tests by the United-States, the former URSS, and the United Kingdom, accidently released a certain number of nuclear by-products in the atmosphere. The isotope $^{137}$Cs display a peak in 1963, accompanied by a smaller peak in $^{241}$Am. The Chernobyl accident in 1986 further dispersed $^{137}$Cs into the northern atmosphere (Appleby, Richardson & Nolan, 1991). These three anchoring points allow a good constraint since 1950 AD.

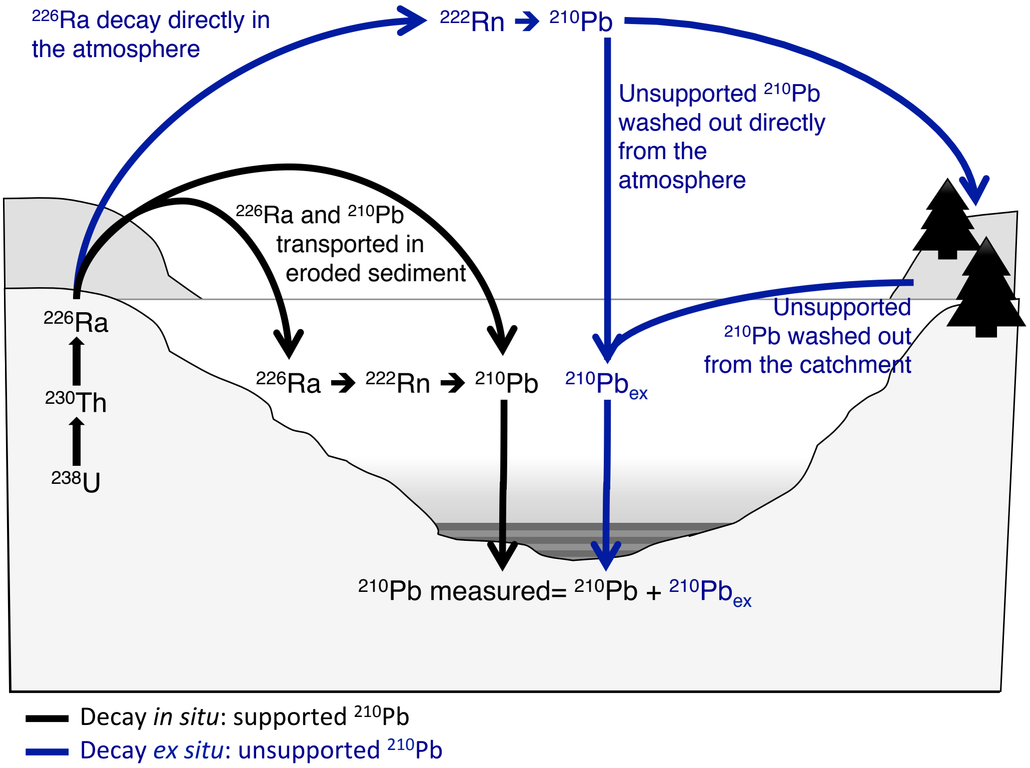


**Figure 1.16 I** Sources of $^{210}$Pb in lake sediment. Adapted from Wilcock (2014).

Independently of human activities, $^{210}Pb$ excess ($^{210}Pb_{ex}$) activity gives an indication on the sedimentation dynamic of the lake. $^{210}Pb$ comes from the disintegration of $^{226}Ra$ in rock and sediment, and from the disintegration of $^{222}Rn$ in the atmosphere. While $^{226}Ra$ and $^{210}Pb$ triggered by erosion from the watershed are in secular equilibrium ($^{210}Pb$ supported), the $^{210}Pb$ product in the atmosphere, by $^{222}Rn$ decay, are remove from the atmosphere by dry and wet fallout and integrated to soils, lakes and sediments ($^{210}Pb$ excess) (Figure 1.16). As a consequence, it is possible to estimate the excess $^{210}Pb$ ($^{210}Pb_{ex}$) coming solely from the atmosphere by subtracting the total $^{210}Pb$ by $^{226}Ra$. The $^{210}Pb_{ex}$ activities follow a regular exponential decay (characterized by its half-life $t_{1/2} = 22.3$ years) from which it is possible to calculate the sedimentation rate.

This dating method is based on the hypothesis that there is neither mixing nor Pb diffusion in the sediment. The constant flux constant sedimentation rate (CFCS) model was then applied (Goldberg, 1963). In a logarithmic diagram $^{210}Pb_{ex}$ activities according to the depth define a linear model. Any instantaneous event has to be removed before computation (low $^{210}Pbex$ values). The method also gives the possibility to detect eventual changes in sedimentation rates.

### 1.3.2.3 | Principle of palaeomagnetic dating

Palaeomagnetic dating is based on the measurement of the secular variations in magnetic fields, to which magnetic particles respond during the sedimentation process. Christian Crouzet, Nicolas Thouveny and François Demory carried out the measurement on Ku-IV (Table 2.2, p85) at the CEREGE palaeomagnetic laboratory (Aix-Marseille University).

In practice, the magnetization vector was measured in the sediment every 4 cm. Particles sediment in a specific position that can be described by a 3-dimension vector. This position is translated in two 2-dimension vectors, namely declination (North, South, West, East) and inclination (up, down).

The declination and inclination curves were corrected for any edge effect (*i.e.* the measurement is less precise on the edge of the core) or rotation (the declination curve can be affected by the fact that during the coring process, the corer may turn). Then, the curves were compared to reference curves from the Arch3k.1 model (Donadini, Korte & Constable, 2009; Korte, Donadini & Constable, 2009). This recent model highly decreased the ages uncertainties for Europe (Figure 1.17) by including a number of data 55 % greater than in previous compilations (Donadini *et al.*, 2009).

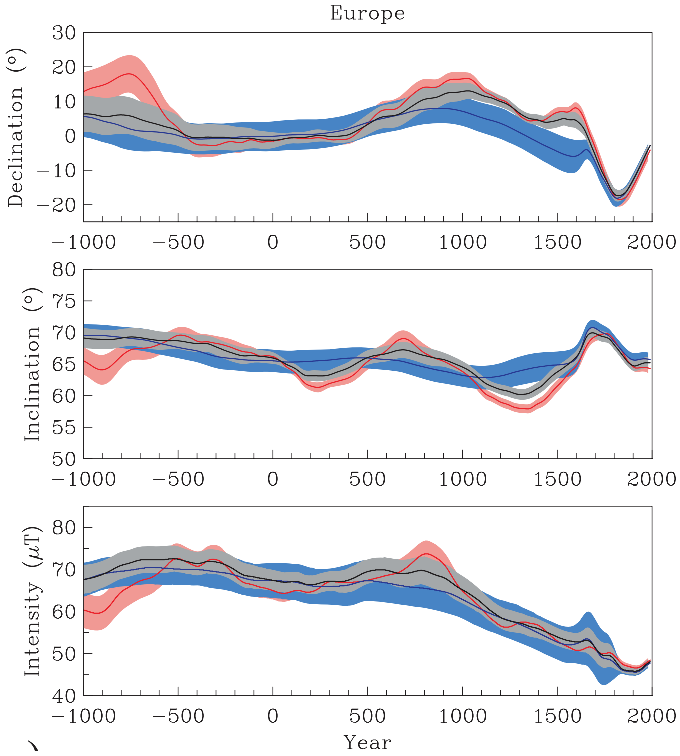


**Figure 1.17 I** Examples of model prediction uncertainties for a location in central Europe (location 50°N, 5°E) for the models ARCH3k.1 (red), SED3k.1 (blue), and CALS3k.3 (black) with shaded uncertainty estimates (from Korte *et al.*, 2009).

Average model prediction and uncertainties have been estimated as standard deviation of the component predictions of the statistically varied models.

### 1.3.2.4 | Magnetic susceptibility for core correlation

Magnetic susceptibility is a complementary measure to palaeomagnetic dating and allows comparing several cores from the same lake. This method is more robust than stratigraphic event correlation.

Marlène Lavrieux measured the magnetic susceptibility at the EAWAG for JOU16-02 (Table 2.2, p85) and JOU13-02, the dated reference core. A comparison of peaks in magnetic susceptibility allowed to project dated horizon on JOU16-02 and build the age model.

### 1.3.2.5 | Varves counting

Varves (*i.e.* annually laminated sediment) present the opportunity to date with an annual precision the sediment sequences that display such sedimentation. Many lakes became varved over the course of the past century as a consequence of the worldwide spread of bottom anoxia (Jenny *et al.*, 2016). Varve counting sometimes allowed confirming radionuclides chronology (e.g. in Lake Geneva and Lake Varese), and sometimes constituted the only dating method (e.g. in Lake Zurich). Irene Brunner and Nathalie Dubois (EAWAG) counted the varves on ZH17-21 (Table 2.2, p85).

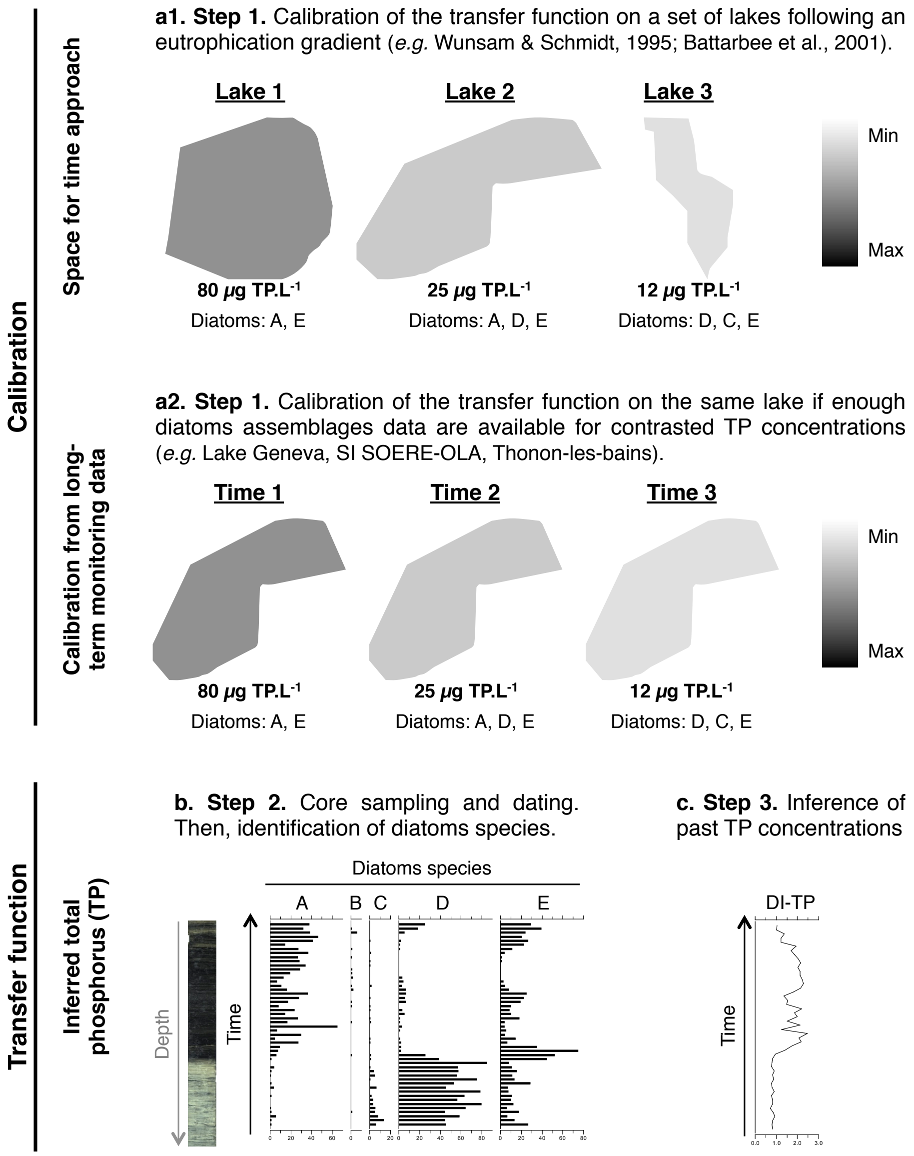
### 1.3.3 | PROXY FOR ECOLOGICAL CHANGE

Deoxyribonucleic acid (DNA) extraction from diatom assemblages presents a challenge at the first step, when silica frustules need to be broken apart to extract DNA (Vasselon *et al.*, 2017). One man's losses being another man's gain, the resistance of plankton exoskeleton present great opportunity in palaeo-ecology. Indeed, diatoms silica frustules and Cladocera (Crustacea, Branchiopoda) chitinous body parts preserve well in lake sediments. Furthermore, their taxonomy and taphonomic taxonomy is well established (Frey, 1964, 1986, Krammer & Lange-Bertalot, 1986, 1988, 1991a b).

As a result, diatoms and Cladocera have been used in many studies aiming at the reconstruction of lakes trajectory. Diatoms, thanks to the diversity of species, have been used to infer past levels of phosphorus (Hall & Smol, 1992; Wunsam & Schmidt, 1995; Battarbee *et al.*, 2001) and pH (Birks *et al.*, 1990). This is based on a 'space for time' approach, where lakes are sampled along an environmental gradient – in these cases total phosphorus (TP) and pH, and an assumption is made that species ecological preferences have stayed the same. Then, species composition is representative of a certain level of pressure, which means that any change in species composition in fact reflect changes in the level of the considered pressure (Figure 1.18). When sufficiently long-term monitoring datasets are available, diatom inferred TP (DI-TP) performance can be improved by crossing the contemporary diatom assemblage, the fossil assemblage, and the TP level (e.g. Berthon *et al.*, 2013; Alric *et al.*, 2013).

Subfossil Cladocera present a lesser diversity that makes them irrelevant for transfer functions. However, their traits (*e.g.* macrophyte associated, pelagic grazer) can inform on the habitats available within the lakes (Bjerring *et al.*, 2009). They are one of the most valuable biological proxies preserved in lake sediments that can be studied for reconstruction purposes (Korhola & Rautio, 2001; Tolotti, Milan & Szeroczyńska, 2016). In lakes, they are present in both the pelagic and littoral zones. They are found with across wide geographical distribution, altitude and system typology. Herbivorous zooplankton grazing plays an important functional role by controlling algal blooms and transferring energy and matter upwards through the food chain (Persson *et al.*, 2007). They have often demonstrated a good sensibility (*i.e.* vulnerability) to eutrophication (Ravera & Parise, 1978; Boucherle & Züllig, 1983), but also change in fish predation pressure (Manca & Ruggiu, 1998) or climatic forcing (Alric *et al.*, 2013; Milan *et al.*, 2017).

Unlike diatoms which frustules are fully preserved (Figure 1.19 a), only body parts of Cladocera are found in the sediment (Figure 1.19 b, Figure 1.20, Table 1.1). It is possible to reconstruct past communities from these body parts (Figure 1.19 c).



**a1. Step 1.** Calibration of the transfer function on a set of lakes following an eutrophication gradient (*e.g.* Wunsam & Schmidt, 1995; Battarbee et al., 2001).

**a2. Step 1.** Calibration of the transfer function on the same lake if enough diatoms assemblages data are available for contrasted TP concentrations (*e.g.* Lake Geneva, SI SOERE-OLA, Thonon-les-bains).

**b. Step 2.** Core sampling and dating. Then, identification of diatoms species.

**c. Step 3.** Inference of past TP concentrations

**Figure 1.18 I** Principle of the transfer function, example with total phosphorus (TP).

(a1) Space for time approach and (a2) calibration from long-term monitoring data. In each case, the diatom assemblage at a specific period is attributed a TP concentrations. (b) Diatom assemblage is reconstructed from a sediment core. (c) Past TP level is inferred under the hypothesis that the specie assemblage respond to TP concentrations.

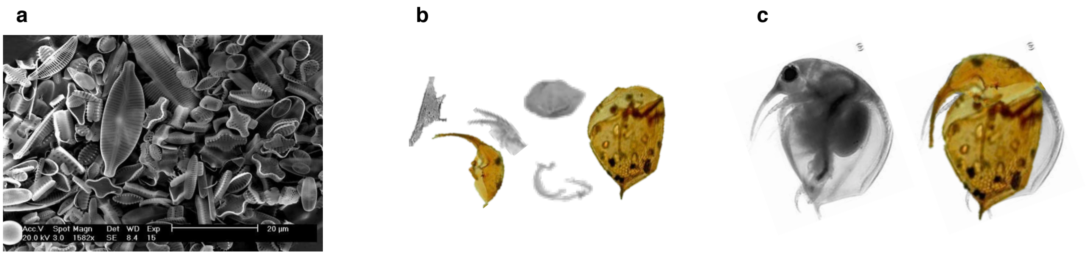


**Figure 1.19 I (a)** Diatoms in lake sediment © Swedish Research Council. **(b)** Subfossil Cladocera © R. Bruel. (**c)** *Bosmina* sp. (left) and superposition of remains found in the sediment **(b)** on the individual (right).

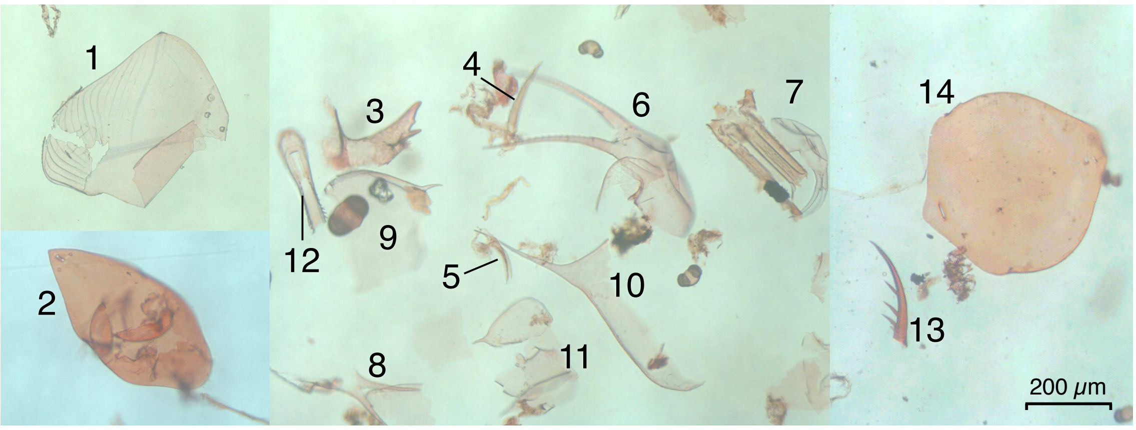


**Figure 1.20 I** Subfossil Cladocera from Lake Lugano sediment core LU-ME-11-1.
Numbers 1 to 14 correspond to identified remains, see Table 1.1 for details.

**Table 1.1 I** Identifications of subfossil Cladocera depicted in **Figure 1.20**, following Szeroczyñska & Sarmaja-Korjonen (2007).

Preservations differ among body parts and species. This is taken in account before counting the total number of individuals by specie. For instance, headshields and valves of *Bosmina* sp. were found in this sub-sample of photos. In total, 3 different individuals were found if we look at the heashields, while 2 individuals were found if we look only at the valves (an unattached valve or an isolated mucro counts as 0.5 individuals). This does not mean that 5 *Bosmina* sp. were necessarily present, as the valves and headshield could come from the same individual. As a result, we take the greater number *i.e.* 3 here. Moreover, because in this subset only *Eubosmina longispina* remains were found, we can accept that the sample only contained this specie. On 14 remains (this subset), this is not significant, but 400 remains were counted by sample to avoid strong bias.

| **No** | **ID** (Szeroczyñska & Sarmaja-Korjonen, 2007) | **Body part** | **Number of individual** |
|---|---|---|---|
| 1 | *Acroperus harpae* | Valve | 0.5 |
| 2 | *Alona affinis* | Headshield | 1 |
| 3 | *Bythotrephes longismanus* | Mandibule | 0.5 |
| 4 | *Daphnia* spp. | Claw | 0.5 |
| 5 | *Daphnia* spp. | Claw | 1 |
| 6 | *Eubosmina longispina* | Headshield | 1 |
| 7 | *Eubosmina longispina* | Headshield | 1 |
| 8 | *Bosmina* sp. | Antennae | 1 |
| 9 | *Bosmina* sp. | Valve | 0.5 |
| 10 | *Bosmina* sp. | Mucro and poorly preserved valve | 0.5 |
| 11 | *Bosmina* sp. | Valves | 1 |
| 12 | *Alona affinis* | Post-abdomen | 1 |
| 13 | *Sida crystallina* | Claw | 0.5 |
| 14 | *Eurycercus* sp. | Headshield | 1 |

### 1.3.4 | STUDY AREA

The ecological dynamic of twelve peri-alpine lakes (Figure 1.21) was reconstructed for the past 50 to 1,450 years using sediment cores retrieved from the pelagic zone (unless stated otherwise). Some Records belong to previously published studies, while others are original data produced during this doctoral work. The same glacial-tectonic processes have carved the lakes of the study during the latest glacial period and lakes formed after the deglaciation 15-10,000 years ago. Their geomorphology varies along the North/South alpine barrier. Lakes at the North have large, deep, U-shaped basins, while lakes at the South have a greater depth to surface ratio, and the largest lakes present different basins. They are submitted to a comparable climate variability for which long-term local meteorological records were available (MeteoSwiss database and HISTALP, Auer *et al.*, 2007). In addition, air temperature anomalies reconstructions were available for the period preceding the $19^{th}$ century, as the Alpine climatic fluctuations have been reconstructed several times using various proxies (Battarbee, 2000; Büntgen *et al.*, 2006).

Extensive studies were carried out on two of these systems, Lakes Geneva (FR, CH) and Varese (IT). They are the focus of Chapters 4 and 5 respectively. The other lakes were studied as part of the Chapter 6. Unpublished data relevant to the study are presented in Chapter 2, and published data are referenced.

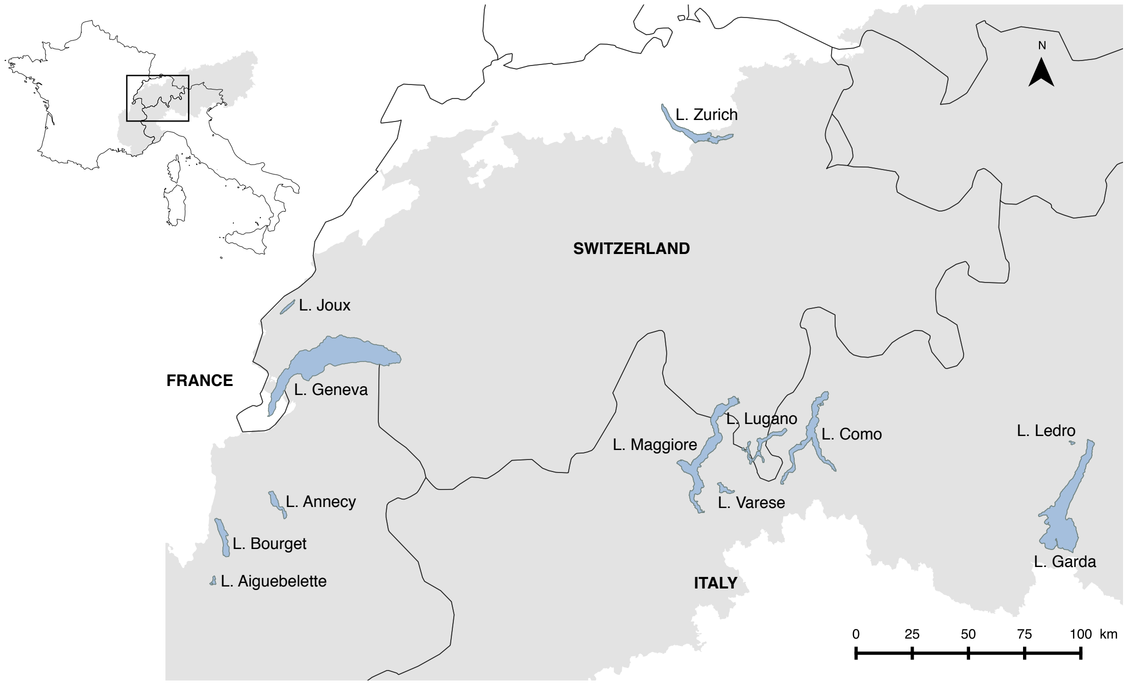


**Figure 1.21 I** Lakes of the study area are peri-alpine lakes located in France, Switzerland and Italy. Grey shading represents the extent of the Alps.

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# Chapter | 2

# Results:

## Study sites

## 2 | RESULTS: STUDY SITES

The purpose of this chapter is to present the results from the analytical part of our research. The remaining chapters focus on our research questions.

A total of twelve lakes were investigated. Two of them were studied extensively and are the purpose of the Chapters 4 and 5. The data for the remaining ten lakes are either original data (Lake Aiguebelette, Lake Joux, Lake Zurich, Lake Lugano, Lake Como) or data published in previous studies (Lake Annecy, Lake Bourget, Lake Geneva short sequence, Lake Garda, Lake Ledro, Lake Maggiore). Several people, listed in Table 2.1, carried data acquisition out over 10 years. Sometimes, analyses were undertaken on more than one core. This is specified in Table 2.2.

**Table 2.1 |** Principal investigators involved in data acquisition.

| Lake | Dating | Pigment analysis | Diatom counting | Cladocera counting |
|---|---|---|---|---|
| **Aiguebelette** | Jean-Louis Reyss | – | – | Mickaël Nicolas |
| **Annecy** | Jean-Louis Reyss | – | Vincent Berthon | Marie-Elodie Perga |
| **Bourget** | Jean-Philippe Jenny | – | Vincent Berthon | Benjamin Alric |
| **Como** | Pierre Sabatier | – | – | Rosalie Bruel |
| **Geneva short-core** | Jean-Philippe Jenny | – | Vincent Berthon | Benjamin Alric |
| **Geneva long-core** | Pierre Sabatier, Stéphanie Girardclos, Katrina Kremer | – | Aldo Marchetto | Rosalie Bruel |
| **Joux** | Marlène Lavrieux, Nathalie Dubois | – | – | Rosalie Bruel |
| **Ledro** | Manuela Milan | – | Manuela Milan | Manuela Milan |
| **Lugano** | Pierre Sabatier | Andrea Lami | Aldo Marchetto | Rosalie Bruel |
| **Maggiore** | Meghan Brown | – | Aldo Marchetto | Liisa Nevalainen |
| **Garda** | Manuela Milan | – | Manuela Milan | Manuela Milan |
| **Varese** | Pierre Sabatier | Andrea Lami | Aldo Marchetto | Anaëlle Bernard & Rosalie Bruel |
| **Zurich** | Nathalie Dubois | – | Aldo Marchetto | Rosalie Bruel |

**Table 2.2 |** Cores used for the different analyses for each lakes of the study.

| Lake | Dating | Pigment analysis | Diatom counting | Cladocera counting |
|---|---|---|---|---|
| **Aiguebelette** | AIG08-04 | – | – | AIG08-02 |
| **Annecy** | 06-01 | – | LDA09-P3 | 06-03 |
| **Bourget** | LDB10-P3 | – | LDB09-P3 | LDB09-P3 |
| **Como** | COMO09-1 | – | – | COMO09-1 |
| **Geneva short-core** | LEM10-P1 | – | LEM10-P6 & LEM11-P14A | LEM10-P8 |
| **Geneva long-core** | Ku-IV & KK8 | – | Ku-IV & KK8 | Ku-IV & KK8 |
| **Joux** | JOU13-02 | – | – | JOU16-02 |
| **Ledro** | Led1-11 | – | Led1-11 | Led1-11 |
| **Lugano** | LU-ME-11-1 | LU-ME-11-1 | LU-ME-11-1 | LU-ME-11-1 |
| **Maggiore** | LM10/box | – | LM98/13A | LM10/box |
| **Garda** | Bren1-09, Bar1-11 & LitG1-13 | – | Bren1-09, Bar1-11 & LitG1-13 | Bren1-09, Bar1-11 & LitG1-13 |
| **Varese** | VAR10-4 | VAR10-10 | VAR10-10 | VAR10-10 |
| **Zurich** | ZH17-21 | – | ZH17-21 | ZH17-21 |

Key parameters (e.g. depth, surface area) for each lake are gathered in a table in Chapter 6. In here, we present the age model and the cladoceran stratigraphy for each lake that has not been the focus of a previous publication. Stratigraphically constrained hierarchical clustering (CONISS; incremental sum of squares, Grimm, 1987) was performed for each to identify major transitions in the assemblage. The number of significant groups in the constrained cluster analysis was determined from the broken stick model (Juggins, 2015).

## 2.1 | LAKE GENEVA 1,450 YEARS SEQUENCE

With the goal to analyse sediment intervals affected and unaffected by major human impact, we built a palaeo-record dataset covering the past millennium using three sediment cores collected in 2010 in the deepest basin of Lake Geneva (see Figure 2.1). This section details the dating of the composite LEM10-CC from two cores (Ku-IV and KK8), as well as the correlation between LEM10-CC and the high-resolution record LEM10-P8 using a well dated horizon and confirmed by cladoceran dynamics (Alric *et al.*, 2013). It was mandatory to obtain a precise dating and narrow the uncertainties linked to the initial dating with $^{14}$C technics because our ultimate objective (as depicted in Chapter 5) was to correlate climatic data to ecological dynamics. Because radionuclides only date the past century, we had to turn to other dating technics i.e. palaeomagnetism.

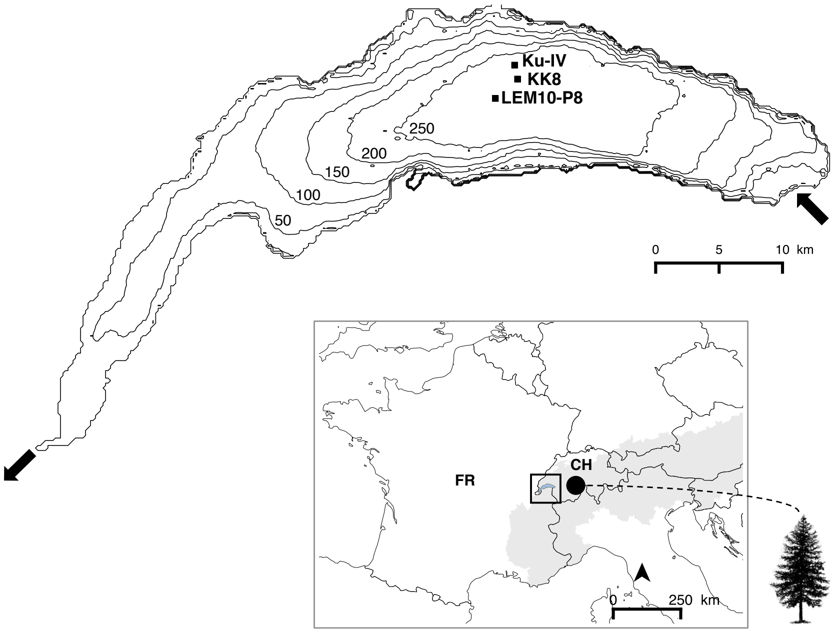


**Figure 2.1 I** Lake Geneva lies at the border between France (FR) and Switzerland (CH) in the peri-alpine domain (Alps as grey surface on the bottom-right insert map).
The bathymetry (in meters) and sediment core localization (black squares) are indicated. Arrows indicate the Rhône river inflow and outflow. The black circle on the bottom insert map shows the location of the four trees-ring sites used by Büntgen *et al.* (2006) to reconstruct SAT anomalies.

The results of this study are the purpose of the Chapter 5. The following information will be published as Supplementary Materials to the manuscript.

## 2.1.1 | Coring & dating: methods

### 2.1.1.1 | Construction of the composite core LEM10-CC

To build a coherent chronology two closely spaced sediment records, Ku-IV (12 m, Long. E 6.60810/ Lat. N 46.47652, sampled on 02/09/2010) and KK8 (12 m, Long. E 6.60810/ Lat. N 46.47652, sampled on 02/09/2010), were merged into one composite core LEM10-CC at the stratigraphic level of turbidite t2 (47.5-51.5 cm on KK8, 54.5-61.5 cm on Ku-IV) as identified by Kremer *et al.* (2014; 2015a) in both records (Figure 2.2). From the previously dated and studied Ku-IV long core, only the sediment sequence situated above the Tauredunum deposit of 563 AD (4.31 upper meters) was analyzed (Kremer, Simpson & Girardclos, 2012).

### 2.1.1.2 | Removal of event layers

The chronology of the composite core LEM10-CC is based on short-lived radionuclide activities, palaeomagnetic secular variations, the coring year and a historical event. From the original 4.21-m-long composite core LEM10-CC (Figure 2.2), seven event layers with thickness above 1 cm were interpreted as instantaneous events (Kremer *et al.*, 2015a). They were thus removed from the raw sequence to construct a 3.93-m-long event-free composite core (Wilhelm *et al.*, 2012). The depth and thickness of these events, and details on the dating methods, are listed in Table 2.3.

**Table 2.3 I** Core depth of event layers in original and composite sediment records along layer thickness. Last column include reference to identified instantaneous events in Kremer *et al.* (2015a) or radiocarbon dated material (Kremer *et al.*, 2012).

| **Core where event layer was originally observed** | **Projected depth** (cm) **in composite LEM10-CC** | **Thickness** of the event layer (cm) | **Correlation with Kremer *et al.*(2015a)** |
|---|---|---|---|
| KK8 | 6 – 7 | 1 | |
| KK8 | 10.4 – 12.8 | 2.4 | |
| KK8 | 47.5 – 51.5 | 4 | t2, Rhône turbidite[8] |
| Ku-IV | 135.5 – 142.5 | 7 | |
| Ku-IV | 162.5 – 166.5 | 4 | |
| Ku-IV | 170.5 – 179.5 | 7 | $^{14}$C age ETH-50442, t4 (Kremer *et al.*, 2015a) |
| Ku-IV | 391 – 393 | 2 | $^{14}$C age ETH-49245 (Kremer *et al.*, 2015a) |

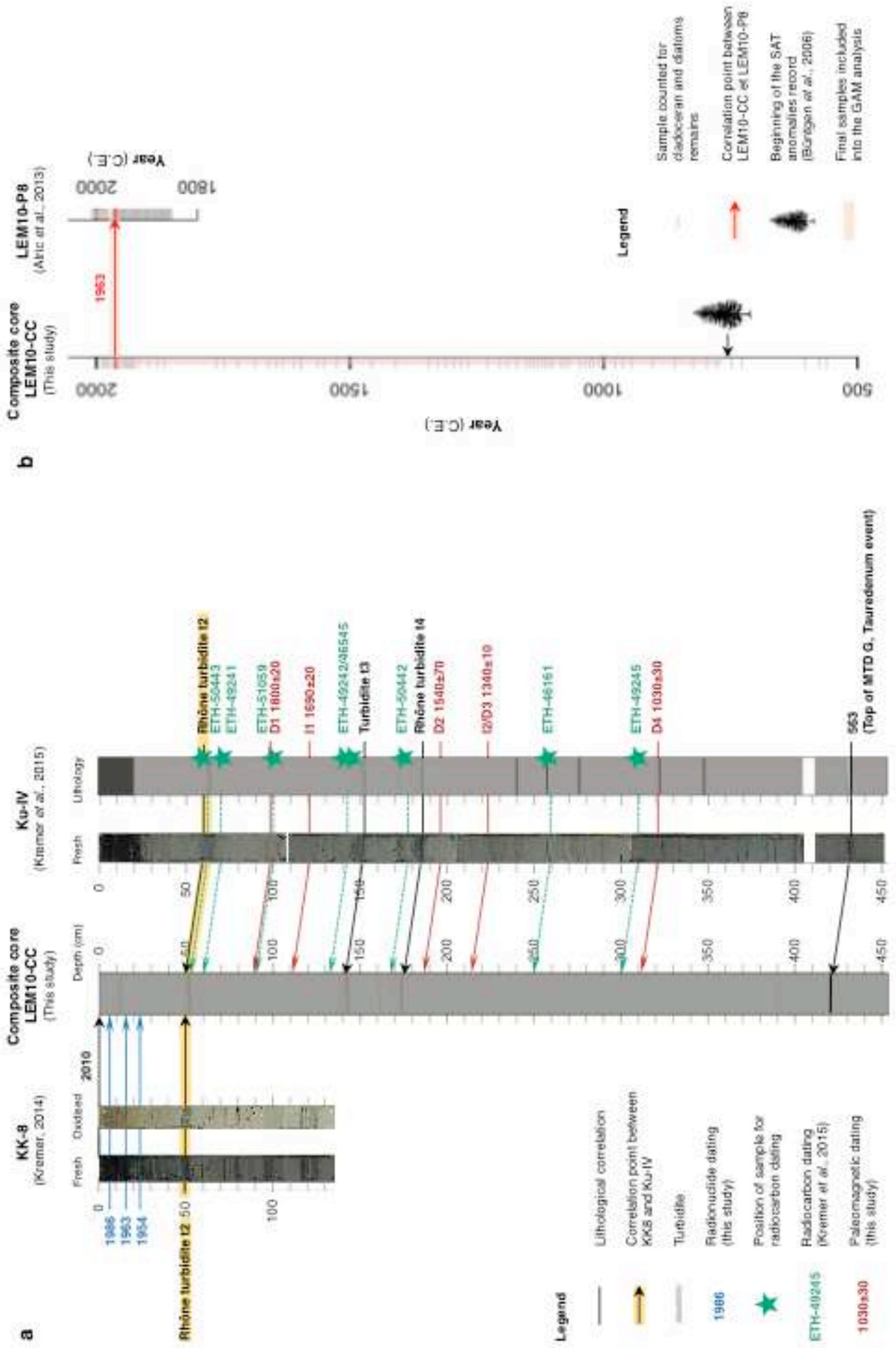


**Figure 2.2 I** Composite core of Lake Geneva.

(a) Construction of the composite LEM10-CC sediment record with core photographs and lithology description used in this study. From left to right, KK-8 (fresh sediment), KK8 (oxidized sediment), LEM10-CC composite core (lithology), Ku-IV (fresh sediment), Ku-IV (lithology). The lithological correlations are represented with black lines and arrows. Dated horizons are represented by blue ($^{137}$Cs activity peaks), red (palaeomagnetism) and green (radiocarbon) lines and arrows, and stars, respectively (see legend); the corresponding ages are written next to the horizons. (b) Construction of the composite cladoceran records between LEM10-CC and the high-resolution LEM10-P8 (Alric *et al.*, 2013) from the well dated 1963 horizons.

#### 2.1.1.3 | Dating from radionuclide activity

The activity of short-lived radionuclides ($^{210}$Pb, $^{226}$Ra and $^{137}$Cs) was measured in the uppermost 43 cm of core KK8, following a non-regular sampling step of 1 to 2 cm, in order to match facies boundaries, and using 0.3–2.4 g samples of dried sediment. Measurements were made by gamma spectrometry, using high-efficiency, very low background, well-type Ge detectors in the Modane underground laboratory (Reyss *et al.*, 1995). The $^{210}$Pb *unsupported* excess activity, ($^{210}$Pbex) were calculated by subtracting the $^{226}$Ra-supported activity from the total $^{210}$Pb activity. We then used the Constant Flux/Constant Sedimentation (CFCS) model applied to the decrease of $^{210}$Pbex to calculate a mean sedimentation rate (Goldberg, 1963). The sedimentation rate uncertainties derived from the standard error of the linear regression of the CFCS model.

#### 2.1.1.4 | Dating from palaeomagnetic secular variations

The natural remanent magnetization (NRM) versus depth was measured in order to compare with known palaeomagnetic secular variations such as Arch3k model (Donadini *et al.*, 2009). Palaeomagnetic investigations were performed on U-channel sub-samples of core Ku-IV, using a 3-axis, 2-G enterprise cryogenic magnetometer at the CEREGE laboratory (Aix-Marseille University, France). The NRM was progressively demagnetized using alternating field (AF) in 10, 20, 30, 40 and 60 mT steps. The demagnetization diagrams (Zijderveld, 1967) showed that behaviour was mainly unidirectional. Principal component analyses and calculation have been performed using puffin plot software (Lurcock & Wilson, 2012) to calculate the Characteristic Remanent Magnetization (ChRM). Measurements affected by side effects (close to U-channel extremities) were removed. We also imparted and demagnetized the samples' anhysteretic and isothermal remanent magnetizations (ARM and IRM respectively) in order to ensure there is no change in magnetic mineralogy (see procedure in Wilhelm *et al.*, 2016). Because the magnetic carrier properties were very stable along the entire studied section, we could be confident in the resulting ChRM direction.

#### 2.1.1.5 | Historical event as stratigraphic marker

The base of the studied sediment sequence is the top of a large basin-wide mass movement deposit that has been related to the historical rockfall of 563 AD (“Tauredunum event”, Kremer *et al.*, 2012).

#### 2.1.1.6 | Radiocarbon dating

Samples of organic macro-remains were analyzed for radiocarbon dating (Kremer *et al.*, 2012).

## 2.1.2 | DATING: RESULTS

### 2.1.2.1 | Chronology from radionuclides activity (1919-2010)

The excess $^{210}$Pb profile measured on core KK8 showed a regular decrease punctuated by two drops in $^{210}$Pbex on the profile (Figure 2.3). Following the lithology and Arnaud *et al.* (2002), these low values of $^{210}$Pbex refer to instantaneous deposits (first two layers listed in Table 2.3) and thus were excluded from the construction of the event-free sedimentary record. $^{210}$Pbex activities plotted on a logarithmic scale revealed two different mean sedimentation rates (SR), respectively of 0.23 ± 0.04 cm.yr$^{-1}$ above 12.1 cm (event-free sequence) and 0.83 ± 0.23 mm.yr$^{-1}$ below this depth. Ages of the original sediment sequence provide a continuous age-depth relationship with a main sedimentation change dated around 1960 AD. With this result, the age of the event layer t2 (turbidite), initially determined from $^{14}$C dating as 1785 ± 115 (Kremer *et al.*, 2015a) is now much better constrained to 1919.7 ± 9.4.

The $^{137}$Cs activity profile of core KK8 reveals two peaks at 5.5 cm ± 5 mm and 15.5 cm ± 5 mm, corresponding respectively to 1986 (Chernobyl accident) and 1963 (atmospheric atomic tests) (Appleby *et al.*, 1991). Below 23.5 cm ± 5 mm, the recorded $^{137}$Cs activities are close to zero, pointing to a sequence deposited before 1955 (first $^{137}$Cs fallout). These three $^{137}$Cs markers are in good agreement with the CFCS age model over the last century, which confirms its reliability (Figure 2.3).

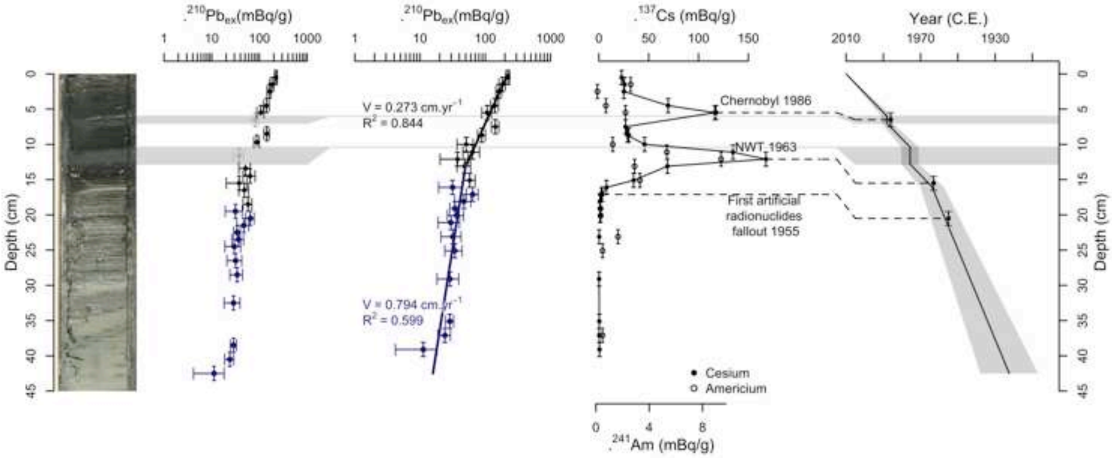


**Figure 2.3 I** Chronology of Lake Geneva sediment core KK-8.

Chronology (with 1σ uncertainties) of the uppermost part of core KK8 based on activity of short-lived radionuclides ($^{210}$Pbex and $^{137}$Cs) and the application of a CFCS model to the event-free sedimentary profile of $^{210}$Pbex (right panel). Uncertainties of $^{137}$Cs activities are included as dots size. Grey bands correspond to event layers / turbidite intervals, interpreted as instantaneous deposits (relatively to the rest of the chronology).

### 2.1.2.2 | Record of palaeomagnetic secular variations

The declination and inclination of the ChRM measured on Ku-IV were compared with those issue for Arch 3k model (Donadini *et al.*, 2009) in order to provide additional and independent age depth coordinates. Assuming NRM is acquired during or immediately after deposition, this comparison with reference curves allowed the identification of two inclination points and four declination points (Table 2.4). Inclination points I1 (1690 ± 20) and I2 (1300 ± 50) were respectively observed at 121 ± 10 cm and 221 ± 15 cm (Figure 2.4) and declination points D1 (1800 ± 20), D2 (1540 ± 70), D3 (1370 ± 40) and D4 (1030 ± 30) were respectively observed at 100 ± 15 cm, 196 ± 15 cm, 224 ± 10 cm and 322 ± 10 cm (Figure 2.5). I2 and D3 were observed for the same depth, thus allowing narrowing the confidence interval of the 224 cm ± 10 cm depth to an age of 1340 ± 10 cm.

**Table 2.4 I** The name of the stratigraphic horizons (ID), the dating method, the age and error (cal. BP) are given along of the original core name, the respective projected depth in raw and corrected composite record LEM10-CC.
(ChRM= Characteristic Remanent Magnetization). *$^{14}$C ages rejected by Kremer et al. (2012). **$^{14}$C ages used to build the age-depth model by Kremer et al. (2012) but rejected in this study in the light of new dated horizons.

| ID | Dating Method | Age cal. BP (yr) | Original sediment core | Projected depth (cm) in LEM10-CC | Event corrected depth (cm) in LEM10-CC |
|---|---|---|---|---|---|
| Surface sediment | Coring year | -60 ± 1 | KK8 | 0 | 0 |
| Chernobyl | $^{137}$Cs | -36 ± 1 | KK8 | 5.5 ± 0.5 | 5.5 ± 0.5 |
| Atomic test | $^{137}$Cs | -13 ± 1 | KK8 | 15.5 ± 0.5 | 12.1 ± 0.5 |
| Before test | $^{137}$Cs | -5 ± 1 | KK8 | 23.5 ± 0.5 | 20.1 ± 0.5 |
| Rhône turbidite t2 (Kremer *et al.*, 2015a) | $^{210}$Pb decay | 30.3 ±9.4 | KK8 | 47.5 ± 0.5 | 44.1 ± 0.5 |
| ETH-50443* | $^{14}$C yr BP | 143 ± 30 | Ku-IV | 52 ± 1 | 44.6 ± 1 |
| ETH-49241* | $^{14}$C yr BP | 614 ± 51 | Ku-IV | 60 ± 1 | 51.6 ± 1 |
| D1 | ChRM | 150 ± 10 | Ku-IV | 90 ± 7.5 | 82.6 ± 7.5 |
| ETH-51059* | $^{14}$C yr BP | 382 ± 35 | Ku-IV | 90 ± 10 | 82.6 ± 10 |
| I1 | ChRM | 260 ± 10 | Ku-IV | 111 ± 5 | 103.6 ± 5 |
| ETH-49242* | $^{14}$C yr BP | 877 ± 59 | Ku-IV | 130 ± 1 | 122.6 ± 1 |
| ETH-46545* | $^{14}$C yr BP | 870 ± 25 | Ku-IV | 135 ± 1 | 127.6 ± 1 |
| ETH-50442** | $^{14}$C yr BP | 198 ± 30 | Ku-IV | 167 ± 1 | 144.6 ± 1 |
| D2 | ChRM | 410 ± 35 | Ku-IV | 186 ± 7.5 | 160.6 ± 7.5 |
| I2/D3 | ChRM | 610 ± 5 | Ku-IV | 214 ± 5 | 188.6 ± 5 |
| ETH-46161** | $^{14}$C yr BP | 870 ± 25 | Ku-IV | 250 ± 10 | 224.6 ± 10 |
| ETH-49245** | $^{14}$C yr BP | 1102 ± 72 | Ku-IV | 300.9 ± 3 | 273.6 ± 3 |
| D4 | ChRM | 920 ± 15 | Ku-IV | 312 ± 5 | 286.6 ± 5 |
| Tauredenum | Historical time marker (Kremer *et al.*, 2012) | 1387 ± 1 | Ku-IV | 421 ± 1 | 393.6 ± 1 |

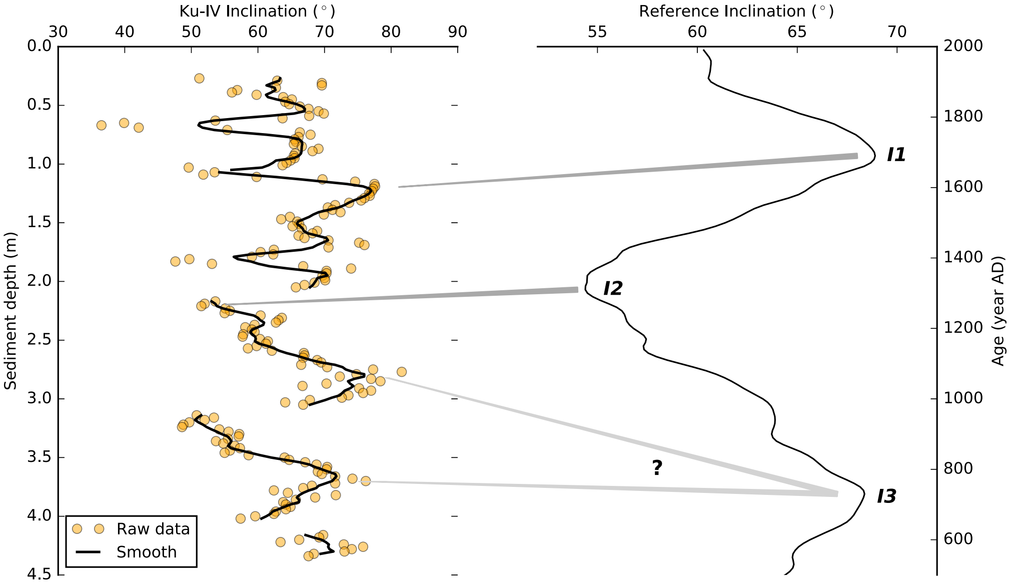


**Figure 2.4 I** Inclination curve of Ku-IV.

Inclination curve of Ku-IV averaged over a 12-cm-window (left panel) and comparison with the reference inclination calculated from Arch3k model (Donadini *et al.*, 2009) for Lake Geneva (right panel). The I1 and I2 inclination points are used in the age-depth model (Figure 2.6)

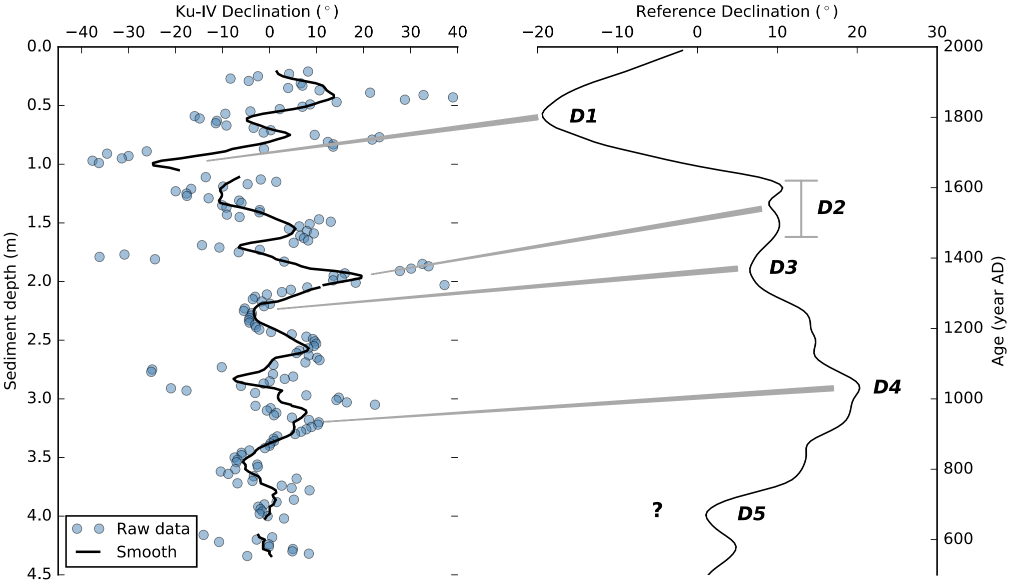


**Figure 2.5 I** Declination curve of Ku-IV.

Declination curve of Ku-IV averaged over a 12-cm-window (left panel) and comparison with the reference declination calculated from Arch3k model (Donadini *et al.*, 2009) for Lake

Geneva (right panel). The D1 to D4 declination points are used in the age-depth model (Figure 2.6).

### 2.1.2.3 | Age-depth model

From the event free composite core LEM10-CC, we calculated a continuous age-depth relationship with the R-code package 'Clam' version 2.2 (Blaauw, 2010b). This age model integrates 11 stratigraphic horizons (Table 2.4): i) the coring year, ii) three time markers from $^{137}$Cs activity, iii) the age of turbidite t2 from $^{210}$Pb activity, iv) five dated points from the new palaeomagnetic study, together with v) the 563 AD historical time marker. The best Clam model was obtained using a smooth spline interpolation with a smoothing term of 0.32 which avoids sudden change in sedimentation rates (Figure 2.6). We also tested the age-depth model using the Bayesian model Bacon (Blaauw & Christen, 2011) with the same input data (Figure 2.7). This independent Bacon model allows a comparison with Clam model and shows that both curves have the same trend. The Clam model was favored because it better fits the original time markers of radionuclides activity that are important for a precise 20th century chronology.

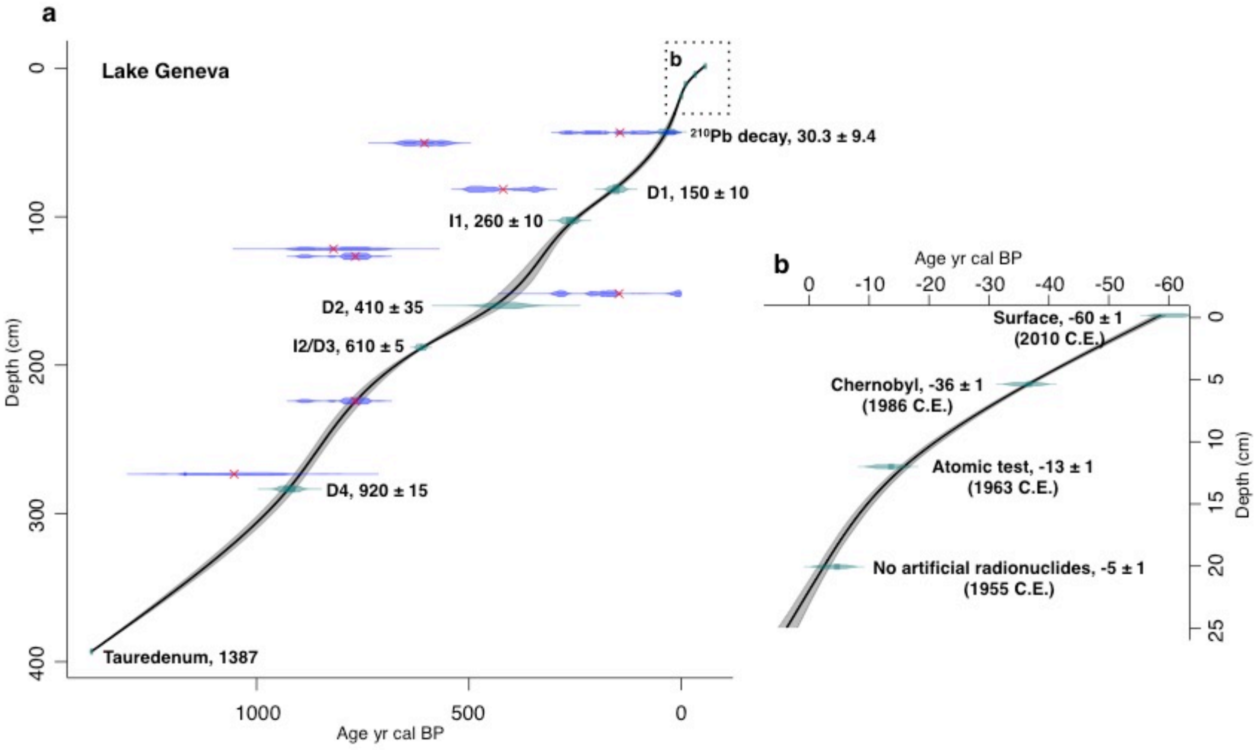


**Figure 2.6 I** Age-depth model of composite core LEM10-CC built with Clam R-code package (Blaauw, 2010a) from 11 stratigraphic horizons.

(a) Total record and (b) zoom on the three $^{137}$Cs dates. Event layers with thickness above 1 cm were interpreted as instantaneous events (Kremer *et al.*, 2015a) and removed before the age model computation. The envelope (grey area) represents the 2-sigma probability interval. Data not used to fit the age model are marked with a red cross.

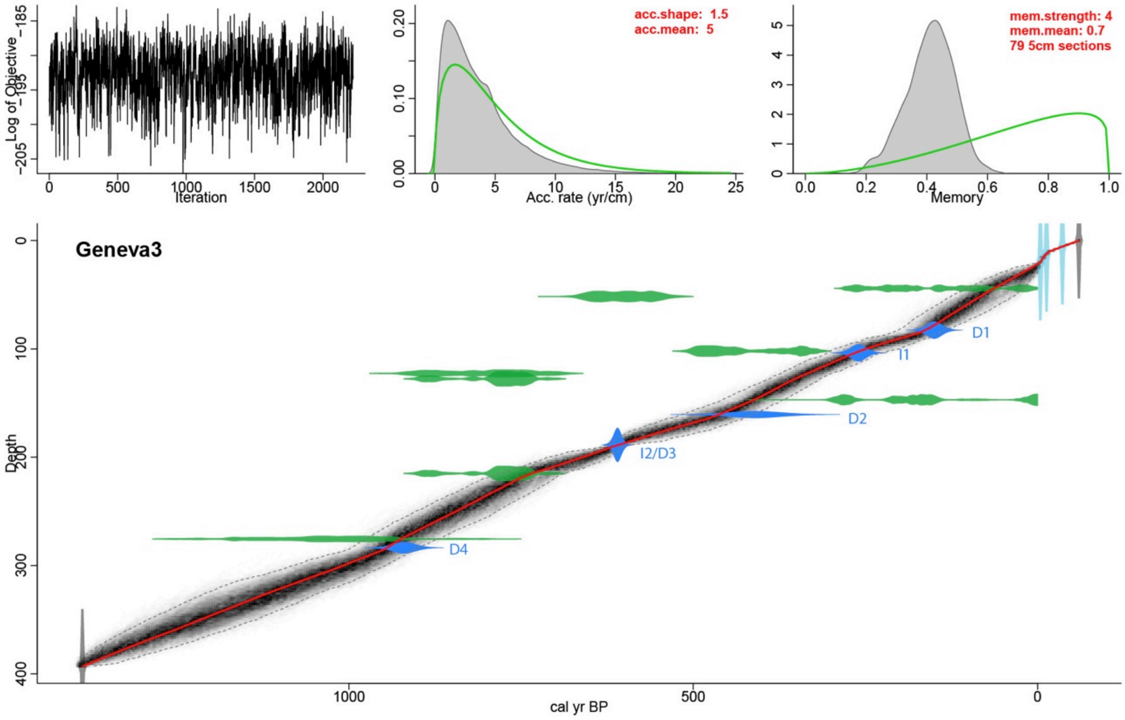


**Figure 2.7 I** Age-depth model of composite core LEM10-CC built with Bacon (Blaauw & Christen, 2011). The upper left panel shows the iteration history, the upper middle panel shows the prior (green line) and posterior (grey area) of the sediment accumulation rate (yr/cm), and the upper right panel shows the prior (green line) and posterior (grey area) of the memory (1 cm autocorrelation strength). The bottom panel indicates the age-depth model. The solid red line represents the single 'best' model based on the weighted mean age for each depth. Associated uncertainties are represented by the grayscale (the darker grey dots are indicative for more likely ages and the dashed black lines indicate the model's 95% probability intervals. The age-depth model is built on the age of the surface sediments (grey) and individual ages obtained from radionuclides (light blue), radiocarbon dating (green) and palaeomagnetism (blue).

## 2.1.3 | VALIDITY OF THE AGE MODEL

### 2.1.3.1 | Fit to dated horizons

The LEM10-CC age model is globally in accordance with the former model of Kremer *et al.* (2015a) that did not benefit from palaeomagnetic data. Yet, the use of palaeomagnetism narrows the initial age model confidence interval and reveals younger ages than previously thought for significant parts of the sediment sequence. Indeed, several $^{14}$C dates appear now notably older than the palaeomagnetic chronology presented herein (Figure 2.6) which is interpreted as the classical effect due to reworking of terrestrial organic matter in the catchment. However, we have to take in account that palaeomagnetic dating may be also affected by the lock-in depth, that expresses the delay in acquisition of the primary magnetization. This would imply that sediments are systematically older than the geomagnetic feature they preserve (Sagnotti *et al.*, 2005; Mellström *et al.*, 2015). While laboratory experiments suggest that post-depositional reorientation is not likely to occur in natural and undisturbed sediments below the sediment-water interface (Katari, Tauxe & King, 2000), it remains difficult to prove it categorically. We chose the palaeomagnetism dating over the $^{14}$C dates because the method provides narrower age-errors. Besides, this palaeo-magnetism model intercepts the age error of the four $^{14}$C retained by Kremer *et al.* (2012), confirming their realism.

The comparison between the Clam- and Bacon-modelled age-depth curves points to the same chronological trend but the Clam model provide a better fit of the radionuclides activity markers. The 20th century chronology is essential in this study, hence Clam-model was chosen.

#### 2.1.3.2 | Sedimentation rates

The resulting sedimentation rates obtained with the Clam age-depth model are of 0.2 cm.yr$^{-1}$ to 0.3 cm.yr$^{-1}$ from 563 to 1913. From 1913 to 1968, sedimentation rate increases as and varies between 0.5 and 1 cm.yr$^{-1}$, corresponding to the change of core, which is interpreted as a difference in compaction due to both different coring methods and porosity. However a drastic - and unexpected for a top core interval- decrease towards smaller values around 0.3 cm.yr$^{-1}$ is observed since the 1960's. Although coring locations of KK-8 and Ku-IV are located distally from the Dranse and Rhone River deltas (Kremer *et al.*, 2015a b), sedimentation rates follows a general trend also observed in seven cores located more proximally to the Rhone River delta (Silva, Girardclos & Loizeau, 2016). Indeed, deep Lake Geneva sediment is mainly driven by changes in the sedimentary load of the rivers (Loizeau & Dominik, 2000). The recent decrease in sedimentation rate observed in this study but also in Silva *et al.* (2016), is certainly related to the decrease in the sediment load of the Rhone River system since the 1960s (Loizeau & Dominik, 2000). This change in sediment load is explained by the strong modifications in the hydrology and sediment routing of the Rhône catchment (Bakker *et al.*, 2017) that happened after the building of several major hydropower systems in Wallis (Loizeau & Dominik, 2000).

### 2.1.4 | CLADOCERA COMPOSITE SUBFOSSIL RECORD

#### 2.1.4.1 | Methods

The cladoceran remains were analyzed for LEM10-CC according to Frey (1986) with the same method as Alric *et al.* for LEM10-P8 (2013). A minimum number of 400 cladoceran remains (headshields, shells, post-abdomens, post-abdominal claws, mandibles and others) were counted and identified per sample using the determination keys of Szeroczyñska and Sarmaja-Korjonen (2007) and an Olympus BX41 microscope at 100-200 magnification. *Bosmina* were determined to the species level (*B. longirostris*, *E. longispina*, and *E. coregoni*), as well as chydorids, whenever possible. Regarding the complexity of the taxa (Alric *et al.*, 2016), *Daphnia* spp. were identified to the genus level. Main changes in the cladoceran assemblage were summarized through stratigraphically constrained hierarchical clustering (CONISS, Grimm, 1987), using R version 3.1.2 (2014-10-31, R Core Team, 2014), as well as the *rioja* package (Juggins, 2015). Finally, a composite cladoceran sequence was created using the most recognizable transition as correlation point.

### 2.1.4.2 | Results

The broken stick analysis performed on CONISS clustering reveals that there were two significant transitions in the cladoceran sequence of LEM10-CC. Those transitions took place in 1961–1963 and in 1930–1934. The assemblage for the 563–1934 period is dominated by the pelagic *Eubosmina longispina* and the ubiquist *Sida crystallina* var. *limnetica* that represent respectively 65% and 25% of the total assemblage on average. From 1934 and within two decades, *Daphnia* spp. replaced *E. longispina* in the pelagic habitat, and *S. crystallina* var. *limnetica* thrived. New rearrangements occurred in 1961–1963 as *S. crystallina* var. *limnetica*, despite being an important species over the 563–1961 period, disappeared from the sediment archive. Since 1963, the community has been dominated by *Daphnia* spp.. *Leptodora kindtii,* which appeared in the record at the same period with very low proportion, represents since the mid-1980s 5–10 % of the assemblage (Figure 2.8).

The major ecological transition in 1961–1963 observed in our record was also evidenced in LEM10-P8 by Alric *et al.* (2013) and the general Lake Geneva species dynamics could really well be matched from one core to the other (*Daphnia* spp. went up from representing 50% to 90%; Figure 2.9). Because we have a high confidence in the dating for this period, thanks to radionuclides dating performed by the same method in the two short cores (Alric *et al.*, 2013), we created the composite core at this date i.e. LEM10-CC until 1961 and LEM10-P8 from 1963 (Figure 2.9). As Alric *et al.* (2013) identified Chydoridae at the family level, we grouped all the remains belonging to this family together to be consistent among the two records. As no particular change in the cladoceran assemblage could be found among the Chydoridae species, that represents always less than 5% of the total assemblage at any given stratigraphic level (Figure 2.9), we have good confidence that key information within the other groups was well preserved.

The difference in abundance (number of individuals per gram of dry sediment) can be explained by the difference of sedimentation rate between the two cores. In the recent most period (post-1960), the sedimentation rate in LEM10-CC is 0.23 cm.yr$^{-1}$ (Figure 2.3), while Alric *et al.* (2013) calculated a sedimentation rate of 0.32 cm.yr$^{-1}$. Hence, the cladoceran remains are less diluted in the LEM10-CC core than in the previous study. This does not affect further analysis as the clustering methods work on the community structure composition for each depth, and both cores display the same representation of the littoral vs. pelagic ratio (i.e. 0.93 and 0.92 for LEM10-P8 and LEM10-CC respectively in 1900).

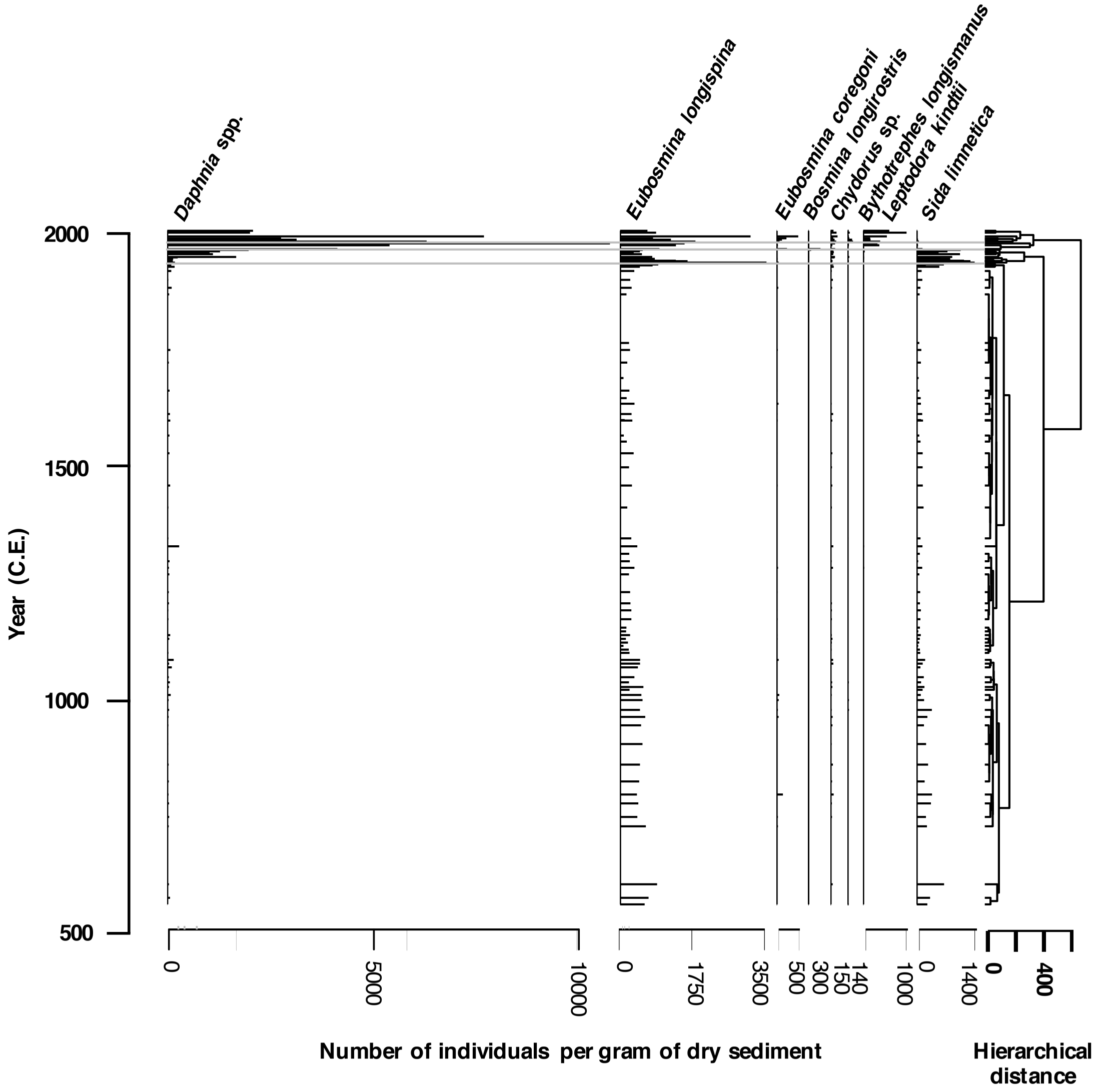


**Figure 2.8** I Palaeostratigraphy of Lake Geneva cladoceran communities from 777 to 2010, with CONISS clustering.

Three major transitions were detected (number assessed by broken stick model) i.e. by order of decreasing significance in 1930 / 1934, 1961 / 1963, and 1990 / 1992.

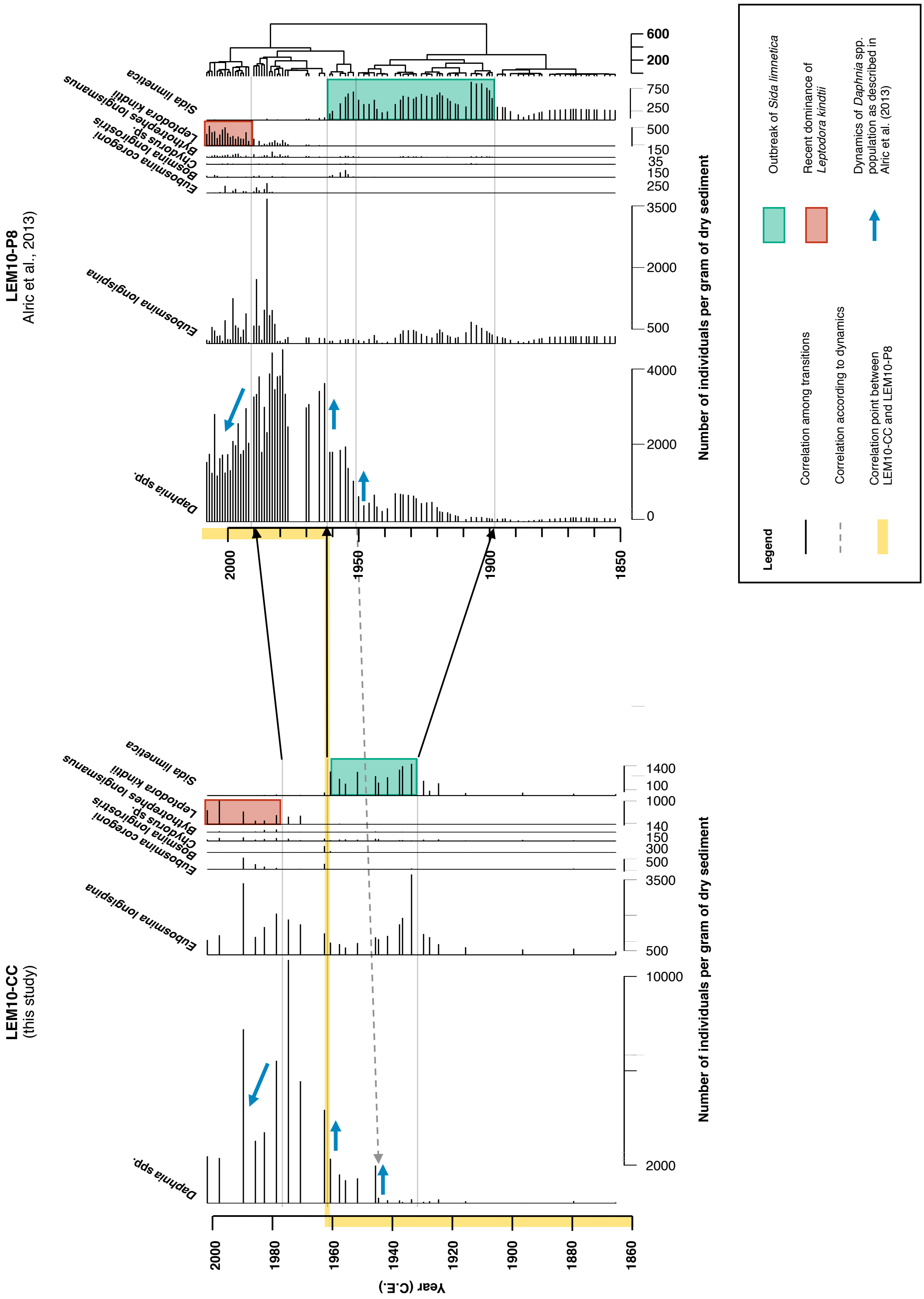


**Figure 2.9 I** Comparison of two records of cladoceran communities in Lake Geneva.
Left: LEM10-CC (this study). Right: LEM10-P8, published data by Alric *et al.* (2013). The LEM10-CC composite core was created from the 1961–1963 transition. Number of individuals per gram of dry sediment.

### 2.1.4.3 | Discussion

As anticipated by working on cores taken in the deep basin of Lake Geneva, pelagic taxa dominate the assemblage (Alric & Perga, 2011). This new insight into Lake Geneva long-term ecological trajectory reveals slightly different results in term of ranking of the major transitions than what was published by Alric *et al.* (2013) i.e. the main transition at the scale of the assemblage becomes the mid-1950s one as opposition with the 1980s one. Yet, the dynamics were really similar, with chronologically an increase in *Daphnia* spp. and *Sida crystallina* var. *limnetica* in the early 1900s, marking the first transition, followed by the total disappearance of the later in the early 1960s. *Daphnia* spp. dominated the assemblage until the 1980s, when its abundance decreases and *Bosmina* sp. as well as predator species (*Leptodora kindtii* and *Bythotrephes longismanus*) became increasingly present in the assemblage. The differences in transition ordering certainly originate from the different weight of the different group. Indeed, the 1400-years insight brought on Lake Geneva assemblage shows that the disappearance of *S. crystallina* var. *limnetica* of the assemblage is really important, while a closer look at the past 150 years understandably promoted the shift of 1950–1952, when *Daphnia* spp. went from representing 20% to 50% of the assemblage, and a shift occurred in the composition of Bosmina remains toward *B. longirostris* dominance. In 1961–1963, the increase in *Daphnia* spp. became even steeper, and the family represented up to 95% of the total assemblage until the late 1900s.

The 1930–1934 transition observed in the LEM10-CC sequence most likely correspond to the 1897–1899 transition depicted in Alric *et al.* (2013). The 30-years discrepancy between the two sequences can be explained by the difference in the age models. As discussed, the dating of LEM10-CC revealed a change of sedimentation rate in the 1960s, confirmed in other studies (Silva *et al.*, 2016), and most likely linked to the impact of hydropower systems on the Rhone river water and sediment dynamics (Loizeau & Dominik, 2000). The dating of Alric *et al.* (2013) sequence did not used any change of sedimentation in the 1960s. This is due to a parsimonious choice done for a short core. The insight brought by the longer KK8 support a change in sedimentation rate. Moreover, the change in mass accumulation rate observed at different distances of the Rhône delta mouth (Loizeau & Dominik, 2000) likely applies to the whole lake. Thus, if instead of choosing a constant sedimentation rate we apply a change in the 1960s to Alric *et al.* (2013) data, all the ages older than 1960 becomes younger, and the 1897–1899 transition observed by Alric *et al.* (2013) falls in the first half of the 20th century instead, corroborating our findings.

The combination of different dating methods crossed with a good knowledge of Lake Geneva sedimentation dynamics (Loizeau & Dominik, 2000) and hydrological historic events (Kremer *et al.*, 2015a b) allowed to build an age model for the sediment record with relatively low age error. This was crucial as we later compared the plankton dynamics reconstructed from the sediment to an independent climatic record (see main text and Chapters 2-3). The necessity to combine three cores is emphasized by the realization that the previous study by Alric *et al.* (2013) did not use the correct ages for the deepest sediment part. While it was not a central part of their study, focusing on the most recent warming episode (since the 1980s), this period was essential for this new study that aims at detecting changes of vulnerability with a tipping-point around the beginning of the Anthropocene as defined by Zalasiewicz *et al.* (2017) i.e. ~1950.

### 2.1.5 | TOTAL PHOSPHORUS IN LAKE GENEVA: LONG-TERM MONITORING DATA AND INFERENCE FROM DIATOMS ASSEMBLAGES

Lake Geneva total phosphorus concentrations (TP) have been measured once or twice a month at the deepest point of the lake since 1958 (Système d'Observation et d'Expérimentation au long terme pour la Recherche en Environnement – Observatoire des LAcs alpins – *http://www6.dijon.inra.fr/thonon/L-observatoire-OLA*). In the first years of available monitoring data i.e. from 1958 (first full year), TP concentrations in the epilimnion were around 12 µg TP.L$^{-1}$ but already within an increasing trend confirming that eutrophication had already started. TP reached 79 µg TP.L$^{-1}$ in 1970, stabilized transiently around 50 µg TP.L$^{-1}$ in the 1972–1986 period, and has been decreasing since then. Current TP concentrations are similar to those measured during the beginning of the monitoring (close to 15 µg TP.L$^{-1}$) (Figure 2.10). In order to extend the TP record beyond 1958, total phosphorus concentrations (0-20 m) were inferred from the composition of subfossil diatoms in LEM10-CC. Previous works on short cores, covering 1880-2010, had confirmed that diatom-inferred TP provide reliable estimates in Lake Geneva (Berthon *et al.*, 2013) and capture changes in epilimnetic (0-20m) TP concentrations above 8 µg.L$^{-1}$.

Diatoms counting were carried out on sub-samples of LEM10-CC. Sub-samples for diatom analysis were cleaned with $H_2O_2$ and HCl following Renberg (1990). Diatom frustules were mounted in Naphrax. On each slide, at least 300 valves were counted and identified by light microscopy, using phase contrast with 1000× magnification, following Krammer and Lange-Bertalot (1986, 1988, 1991a b). Description of changes in the diatom assemblage was done resorting to stratigraphically constrained hierarchical clustering (CONISS), using R version 3.1.2 (R Core Team, 2014), as well as the *rioja* package (Juggins, 2015). Mean total phosphorous concentrations were reconstructed from a diatom-based inference model based on 345 surface sediment samples collected in lakes in Europe along a trophic gradient (http://craticula.ncl.ac.uk/Eddi, Battarbee *et al.*, 2001). The calibration dataset covered a large trophic gradient, with mean annual TP ranging from 2 to 1189 µgP.L$^{-1}$. Reconstruction was performed, using weighted averaging with inverse deshrinking (ter Braak & van Dame, 1989). The root mean squared error of prediction (RMSEP) was calculated for each sample set using bootstrapping with 1000 cycle. Diatom profiles and lake DI-TP reconstruction were performed using program C2 (version 1.7.2, Juggins, 2007).

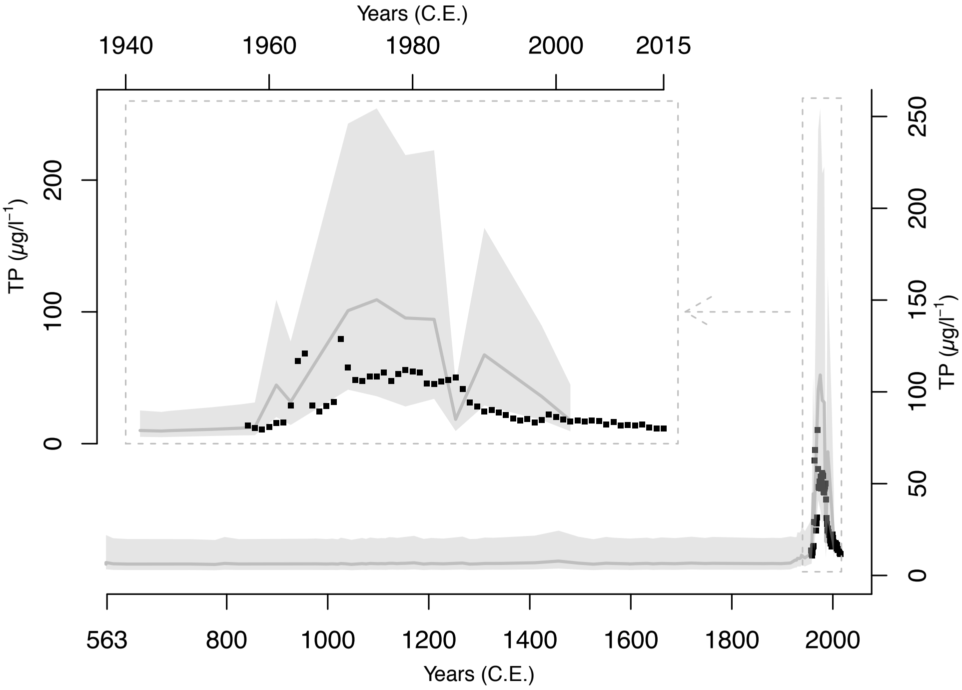


**Figure 2.10 I** Total phosphorus (TP) in Lake Geneva.

Solid grey line corresponds to diatom inferred TP (DI-TP) from LEM10-CC core. Grey envelop depict the interval of confidence (95%) of the DI-TP, calculated by bootstrap with 1000 iterations. Black squares are epilimnic TP from long-term monitoring (1958–2015, SOERE OLA). The top-left graph shows the detail for the 1940-2015 period.

The palaeo-record, on which a hierarchical CONISS analysis was performed, revealed two significant changes in the subfossil diatom assemblage of Lake Geneva between 563 and 2010, and both took place in the 20$^{th}$ century (1916 / 1925 and 1952 / 1956) (Figure 2.11). Before 1916, the assemblage was largely dominated by the centric species *Pantocsekiella comensis* (70-80 %), seconded by *Lindavia bodanica* (5-10 %), both species typical of oligotrophic waters. The subfossil diatom record had been stable for the whole 1400 year-long record (Figure 2.11). Only a slight 8% increase of *Pantocsekiella costei* during the 11$^{th}$ century was worth noticing. Inferred-TP were thereby stable and low (< 14 µg.L$^{-1}$) before the 20$^{th}$ century, typical for an oligo/oligomesotrophic lake. From 1925 and up to 1952, *P. comensis* got substituted by *Pantocsekiella costei,* another specie affiliated to nutrient poor waters. *Fragilaria crotonensis* made up to 50% of the assemblage. *F. crotonensis* is somewhat distinctive of waters with higher nutrient levels. The increased contribution of *F. crotonensis* could thereby illustrate a slow and slight increase in TP as soon as the 1920s. Thereby inferred TP remained below 14 µg.L$^{-1}$ for this time-period, excluding any important human driven change in TP in the lake before the 1950s. The second transition in in 1952 / 1956 marked the loss of *Pantocsekiella* sp., while *F. crotonensis* declined in favor of *Stephanodiscus binderanus* that represented up to 74% of the assemblage in 1971. This specific succession is typical for eutrophication and not surprisingly, inferred TP increased up to 109 µg.L$^{-1}$ in 1979, mirroring measured trends in total phosphorus concentrations. Not significant at the time-scale of the study, was the recent reorganisation (in the four-top-most samples of LEM10-CC i.e. reflecting a change in the interval of 1983 / 1986) with a return of *Pantocsekiella* sp. (< 20% vs. > 70% before 1916), and new species i.e. *Asterionella formosa* and *Diatoma tenuis.* The most recent part of the record thereby reflected the recent abatement in water TP. The good coherence between DI-TP and measured TP, as well as the confidence in the age models, allowed the creation of a composite TP record (thereafter referred as to inferred TP, I-TP). DI-TP was used up to 1958 and monitoring data thereafter, avoiding any uncertainties linked to reconstructions.

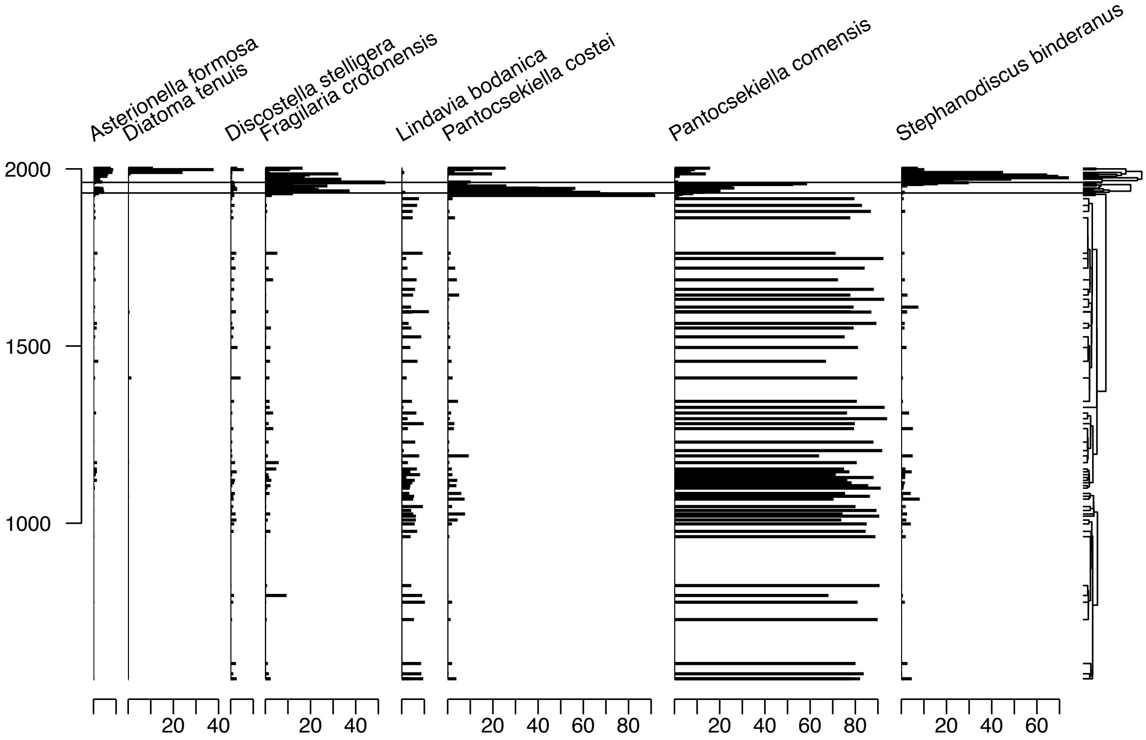


**Figure 2.11 I** Summary diatom stratigraphy of the most common taxa in Lake Geneva LEM10-CC sequence.

The horizontal lines mark the two significant changes in diatom assemblage at the scale of the study.

## 2.2 | THE *FRENCH* LAKES

Lakes Annecy, Bourget and Aiguebelette are the three other large French peri-alpine lakes after Lake Geneva. Reconstruction of the ecological dynamics for these four lakes was carried out with the same methodology in the framework of the program IPER-RETRO funded for the 2009-2014 period (see Perga *et al.*, 2015 for a synthesis). The program was designed in order to evaluate how variations in the intensity of local forcings can affect lake responses to similar climate variability, by comparing the ecological trajectories of different lake habitats for three of the four lakes (Geneva, Annecy, and Bourget). Only references to the papers presenting the conclusions are mentioned thereafter. The data from Lake Aiguebelette were never published and are therefore presented more extensively.

### 2.2.1 | LAKE GENEVA SHORT RECORD, LAKE ANNECY, LAKE BOURGET

#### 2.2.1.1 | Coring and dating

Dating of the high-resolution sequences of lakes Annecy and Bourget are respectively published in Perga *et al.* (2010) and Alric *et al.* (2013). Briefly, sediment dating was performed from one reference core for each lake using radionuclide activity ($^{210}$Pb, $^{226}$Ra, $^{137}$Cs, and $^{241}$Am activities) and confirmed by counting of annual laminations. The cores cover at least the previous century.

#### 2.2.1.2 | Local and global drivers

These three subalpine lakes have the same glacial-tectonic origin and are located within 70 km from each other. They share a common human history of increased local forcings (yet at different intensities) over time over the last 150 years. The increased human population density on their watershed triggered eutrophication from the 1930s to the mid-1970s. The similarities among these lakes stop where the management decisions start. Indeed, eutrophication was directly tackled in Lake Annecy where maximum TP concentrations never exceeded 25 $\mu$gP.l$^{-1}$. In Lake Geneva, differential timing in legislation between Switzerland and France translated in a more severe eutrophication of the lake (max TP= 90 $\mu$gP.l$^{-1}$). Finally, Lake Bourget reached the highest levels of TP (max TP= 110 $\mu$gP.l$^{-1}$), until drastic management decisions were undertaken in the late 1980s with the construction of pipes to deviate wastewaters. Overall, phosphorus inputs from their watersheds have then been successfully abated in the second half of the 20th century and onwards (Figure 2.12).

The SOERE OLA-IS, INRA Thonon-les-Bains, CIPEL (2017-03-21), developed by the INRA Eco-Informatics ORE, gave access to the long-term monitoring data from Lakes Geneva, Bourget and Annecy. The DI-TP reconstructions for the three lakes are published in Berthon *et al.* (2013).

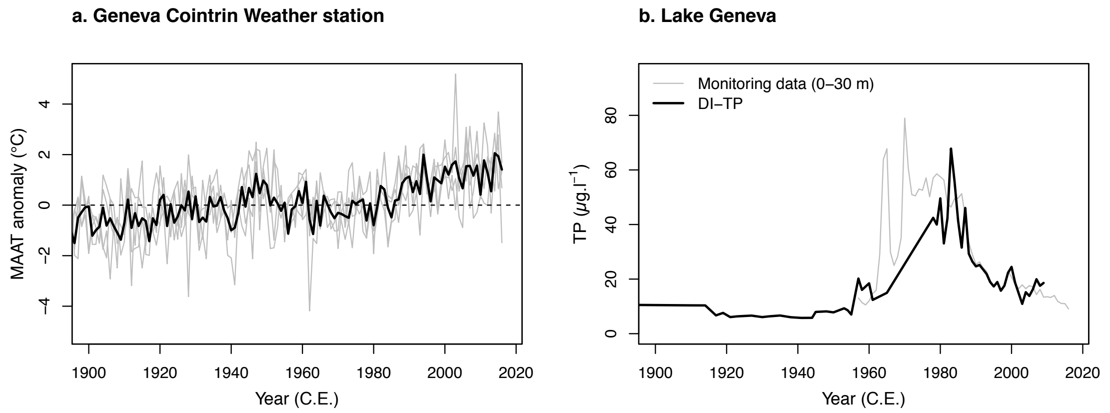
#### 2.2.1.3 | Cladocera

The cladoceran data are published in Perga *et al.* (2010) and Alric *et al.* (2013).

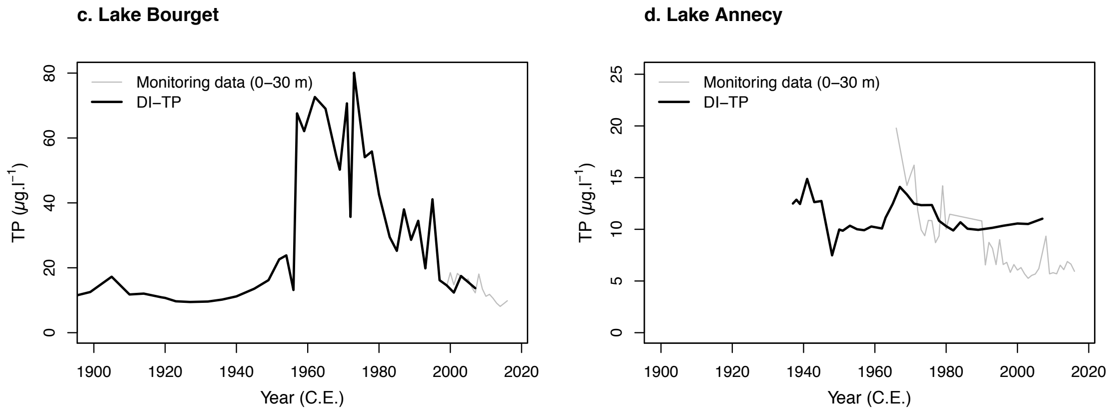
### 2.2.2 | LAKE AIGUEBELETTE

Lake Aiguebelette sediment sequence was analysed using the same methods as in Lake Annecy, Bourget and Geneva, for similar research questions. The project was the purpose of a master thesis by Mickaël Nicolas (2008).

Lake Aiguebelette is the second smallest lake (5.45 km$^2$) of the study at the western-most part of the study area. Lake Aiguebelette is a private lake, which management was entrusted to local community of communes (five in total). Motorboats are forbidden on the lake since 1967 to protect the local environment. Lake Aiguebelette has become the first regional natural freshwater reserve in France in March 2015.


a. Geneva Cointrin Weather station

b. Lake Geneva


c. Lake Bourget

d. Lake Annecy

**Figure 2.12 |** Environmental data French lakes.

(a) Weather data from Geneva Cointrin station. Grey lines show seasonal temperature anomalies and black line shows the mean annual air temperature (MAAT) anomaly. (b, c, d) Monitoring data (grey line) and diatom-inferred total phosphorus (DI-TP, black line) for Lakes Geneva, Bourget and Annecy.

### 2.2.2.1 | Coring and dating

Four sediment cores were taken on 09/01/2008 with a gravity corer in the Southeast pit of the lake (z= 71 m, 5°48.11E – 45°32.996N). AIG08-04 (170 cm) and AIG08-02 (70 cm) were respectively used for dating (radioelements activities measurement) and biological analyses. The age-depth model for AIG08-04 is presented in Figure 2.13.

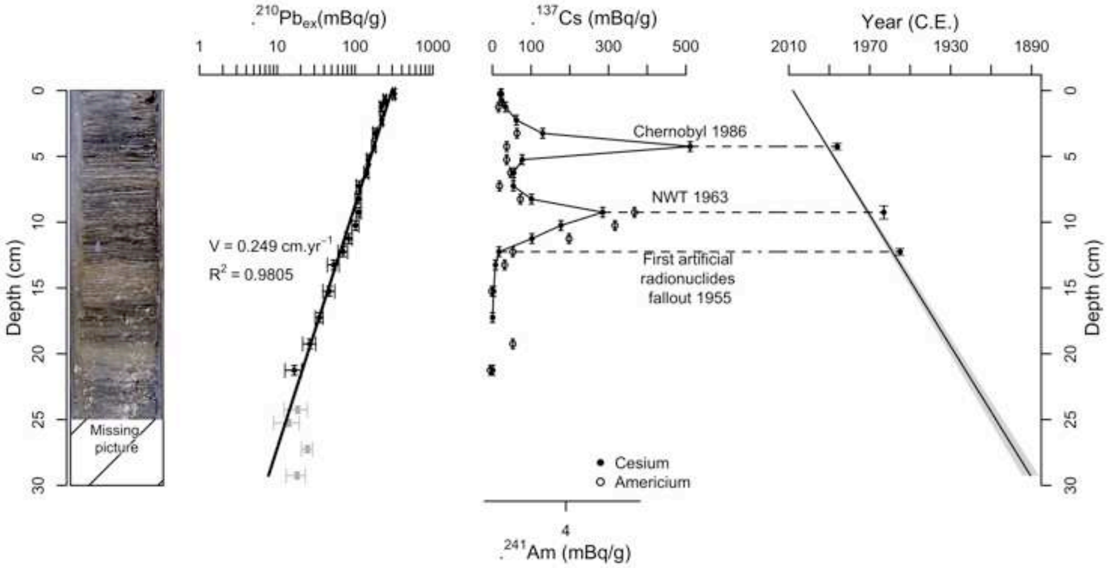


**Figure 2.13 I** AIG08-04, reference cores for dating.

From left to right: photography, $^{210}Pb_{ex}$ activity, $^{137}Cs$ activity, and the age model for the upper 30 cm. The $^{210}Pb_{ex}$ activity points in grey were not included in the sedimentation rate calculation because the low counting time was too low and led to large uncertainties at 1 σ. NWT stands for Nuclear Weapons Testing.

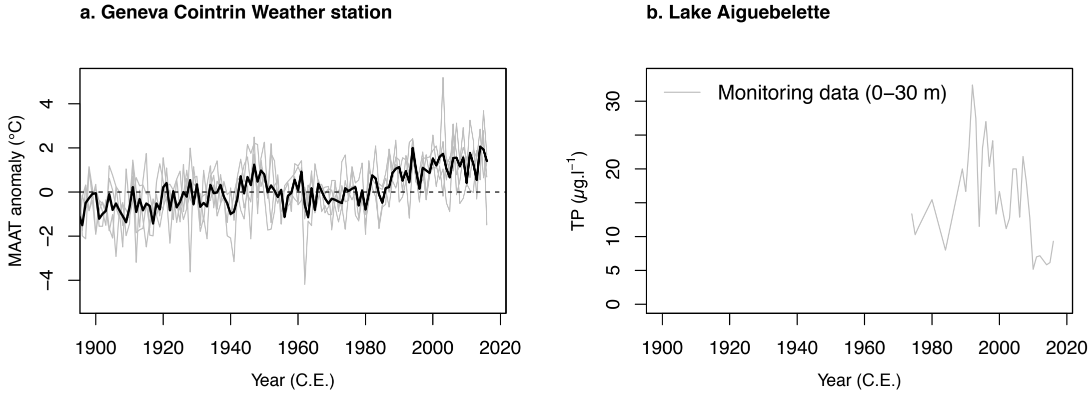


**Figure 2.14 I (a)** Weather data from Geneva Cointrin station. Grey lines show seasonal temperature anomalies and black line shows the mean annual air temperature (MAAT) anomaly. **(b)** Monitoring data (grey line) for Lake Aiguebelette.

### 2.2.2.2 | Local and global drivers

Degradation of water quality was reported as soon as 1950s, with hypoxia of the bottom of the lake during the stratification periods (Dottrens, 1951; Blake & Lascombe, 1978). Monitoring data indicate a relatively low TP level in the epilimnion in the late 1970s (first data) and a maximum eutrophication in the 1990s (Figure 2.14).

The SOERE OLA-IS, INRA Thonon-les-Bains, CIPEL (2017-03-21), developed by the INRA Eco-Informatics ORE, gave access to the long-term monitoring data from Lake Aiguebelette.

### 2.2.2.3 | Cladocera

Cladoceran remains were analysed with the same methods than previously described for Lake Geneva. CONISS clustering identified two significant changes in the cladoceran assemblage of Lake Aiguebelette (Figure 2.15). From 1833 to 1890, the assemblage was characterized by the presence of pelagic grazers, mainly the small *Bosmina longirostris*. From 1894 to 1924, the total abundance of cladocera increased. CONISS detects changes in composition; hence it is the shift toward larger grazers in both pelagic (*Eubosmina longispina*) and littoral (*Sida crystallina*) habitats that marks this period. The major transition took place between 1924 and 1929, and since then (1929-2007 period, the pelagic assemblage is dominated by *Daphnia* spp. At the scale of the past 180 years, *Leptodora kindti* was present in the sediment only for the past 30 years.

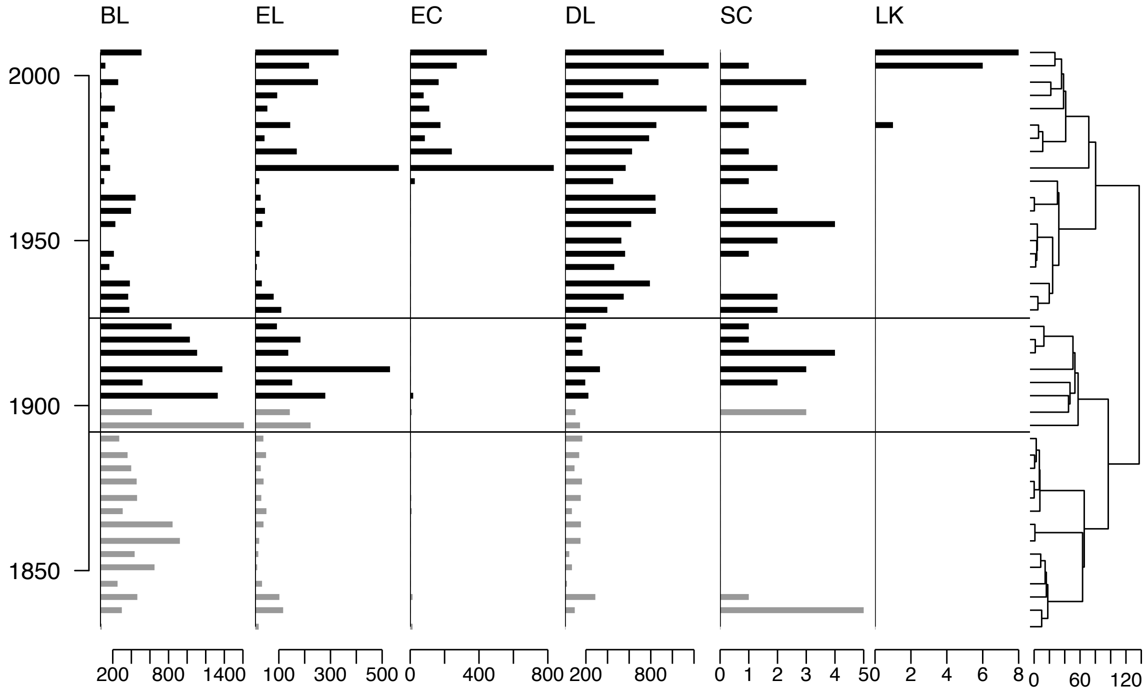


**Figure 2.15.** Stratigraphic abundance of cladoceran remains in Lake Aiguebelette sediment core AIG08-02.

All littoral taxa were merged into a same groups, Chydoridae, to make the plot more readable. Abbreviations: BL= *Bosmina longirostris,* EC= *Eubosmina coregoni*, EL= *Eubosmina longispina*, DL= *Daphnia* spp., LK= *Leptodora kindti*, SC= *Sida crystallina*. The black bars represent the sample >1900 and the grey bars represent the sample <1900.

## 2.3 | LAKE VARESE

### 2.3.1 | GENERAL

Two sediment cores (VAR 10.4 89 cm-long; VAR10.10 63 cm long) were collected in 2010. They were respectively used for dating (radioelements activities measurement) and biological analyses. Cores were sliced at a 1-cm interval for diatoms and cladoceran counting and pigments measurements. Age-model and cladocera profiles are presented in Bruel *et al.* (2018), Chapter 4.

### 2.3.2 | INFERRED TOTAL PHOSPHORUS

#### 2.3.2.1 | Methods

Mean total phosphorous (TP) concentrations were reconstructed from the combination of a pigment and a diatom-based inference model. Sub-samples for diatom analysis were prepared as described in 2.1.5 | p23.

Insights provided by diatoms were reinforced by resorting to ubiquitous pigment analysis. Dry mass (DM – 60°C for 48 h) and loss on ignition (LOI – 550°C for 4 hours) were quantified for each sample. The algal and bacterial pigments were extracted and quantified as described by Lami and colleagues (2000). Individual carotenoids were quantified with High Performance Liquid Chromatography (HPLC) using a ThermoFisher Ultimate 3000 system and the method described by Lami *et al.* (1994). The total carotenoids were used to infer the past total phosphorus concentration (Carotenoid-inferred TP: CarI-TP) according to Guilizzoni *et al.* (2011).

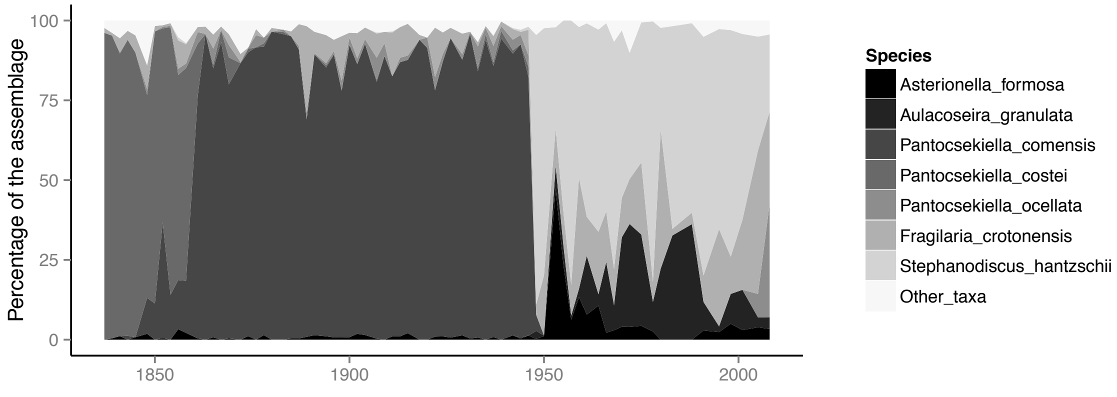


**Figure 2.16 I** Main diatom taxa contributing to the total fossil assemblage of Lake Varese.

For clarity, only species contributing > 1 % to the total diatom assemblage are plotted (i.e., species found in >3 samples or taxa that contributed to 4 % of the total average maximum).

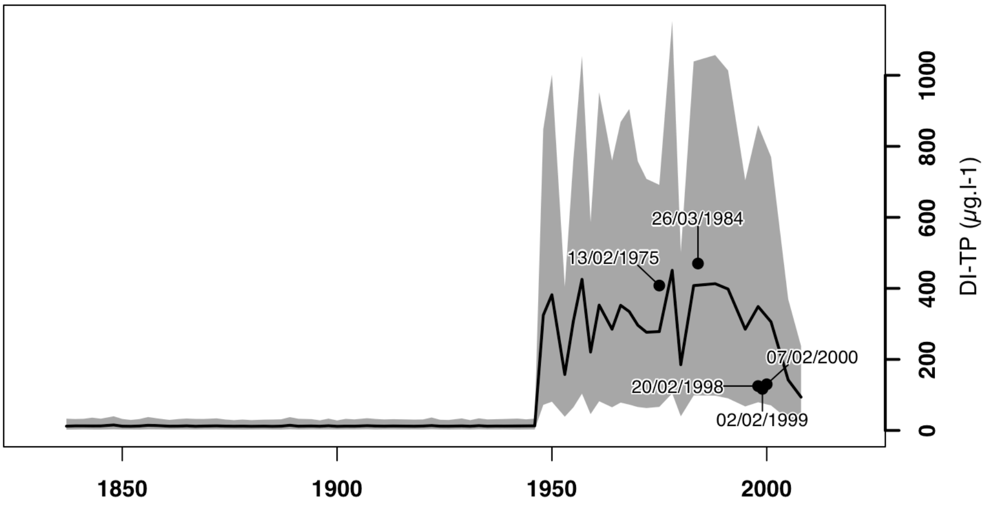


**Figure 2.17 I** Diatom-inferred total phosphorous concentrations in Lake Varese.

DI-TP (plain line), RMSEP (5-95 %) resulting from bootstrapping with 1000 cycles (shaded area) and monitoring data of total phosphorus (· data points).

### 2.3.2.2 | Results

The reconstructed TP dated the transition at 1946 / 1948, from which DI-TP goes from < 5 µg P.l$^{-1}$ (*Cyclotella comensis* characteristic of oligotrophic water (Reynolds, 1984)) to 226 µg P.l$^{-1}$ (assemblage dominated by *Stephanodiscus hantzschii*, which is typical for hypereutrophic lakes) (Figure 2.16, Figure 2.17). The demographic data suggest that this period had one of the most dramatic increases in population around Lake Varese (Archivio di Stato di Milano).

The concentrations of total carotenoids increased as early as the 1870s (Figure 2.18), which indicates a more gradual eutrophication process than what could be reconstructed from DI-TP. From the mid-1940s, photo-pigment concentrations indicated a striking increase along with DI-TP, which is indicative of a nutrient-driven increase in algal biomass. The maximum values were achieved in the 1950s, and again in the mid-1980s, and stabilized at one-half or three-fourths of their maximum over the latest two decades, which mirrored the relative decrease in DI-TP. The CarI-TP indicated a minimum concentration of 9 µg P.l$^{-1}$ and a maximum of 25 µg P.l$^{-1}$ until 1946, which was followed by an increase of up to 47 µg P.l$^{-}$1 in 1948. The chlorophyll *a* to phaeophytin *a* (its principal degradation product) ratio did not indicate any consistent stratigraphic trend, which suggests a constant degradation rate along the core (Leavitt & Carpenter, 1989). The higher value in the top-most portion reflects the recent occurrence of sedimentation.

### 2.3.2.3 | Discussion

Juggins et al. (2013) noted that a number of calibration datasets for diatoms infer secondary gradients and not the major gradient affecting diatom species composition. Indeed, weighted averaging calibration assumes that the species respond to an environmental gradient (e.g., [TP]) according to a Gaussian distribution and that the taxa with an ecological optimal TP close to that of the lake will occur with greater abundance. However, the calibration used was mainly based on the classic trophic sequence from *Cyclotella* to *Asterionella/Fragilaria crotonensis* to *Stephanodiscus* (Harris, 1987), which reflects the known ecology of the main planktonic diatoms (Willen, 1991; Hall & Smol, 2010) and was, therefore, considered reliable (Juggins *et al.*, 2013, page 384). The reliability of the diatom inferences based on this sequence has been shown in the present study and elsewhere by comparing the DI-TP with historical TP values (e.g., Marchetto & Bettinetti, 1995; Marchetto & Musazzi, 2001). Yet, in this case, DI-TP does not accurately reproduce the pre-eutrophication process, as suggested by an increased concentration of total carotenoids in the mid-1920s (Figure 2.18). Indeed, CarI-TP matched the oligotrophic state well but also suggested a slow eutrophication process earlier than the DI-TP, which justified a multi-proxy approach. While pigments are known to be sensitive to early changes in pressure (McGowan *et al.*, 2005; Bunting *et al.*, 2016), CarI-TP was less efficient as soon as Lake Varese became hypereutrophic because phosphorous was no longer a limiting factor.

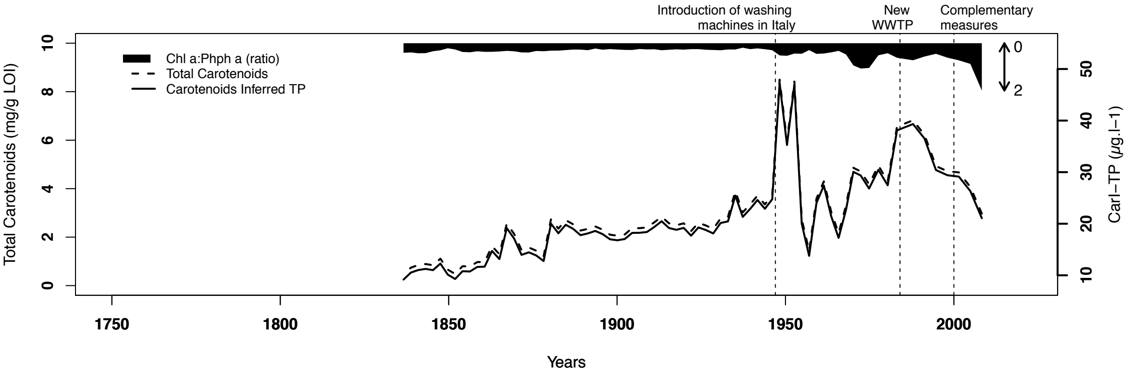


**Figure 2.18 I** Evolution of the total carotenoids (dotted line, primary axis) and carotenoid inferred total phosphorus (CarI-TP, plain line, secondary axis) concentrations in Lake Varese.

Chl a:Phph a is the ratio of chlorophyll a to phaeophytin a (dark area, ranging between 0.19 and 1.95) and is an indicator of the pigment degradation rate along the core.

A composite TP reconstruction was thus used. CarI-TP was used until 1946, whereas DI-TP was used from 1948 (Figure 2.19).

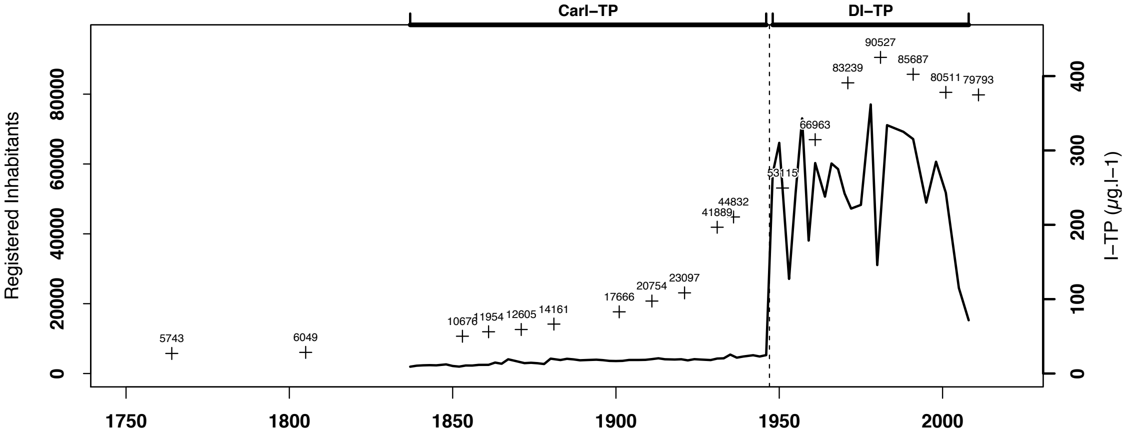


**Figure 2.19 I** Registered inhabitants in the city of Lake Varese over the past 250 years and a composite Inferred TP (I-TP).

(+ data points, primary axis; the source of the demographic data was the Archivio di Stato di Milano – *Statistiche I.Stat* – ISTAT; the URL was last consulted using Wikipedia for data on December 28th, 2012, **www.dati.istat.it)**.

## 2.4 | LAKE COMO

Lake Como (198 m a.s.l.) is located in North-Italy, Lombardy, in the Insubrian Southern Alps and Prealps. Its surface is 142 km$^2$, and its wide catchment covers ca. 4522 km$^2$. The lake is composed of three branches: the northern, the western (Como branch, where the core was sampled) and the eastern (Lecco branch). The Adda River is the main tributary, reaching the lake in the North-sector, and is also the only emissary, outflowing at the end of the Lecco branch.

### 2.4.1 | CORING AND DATING

A 38-cm core (COMO-09-01, 45°49′3.38″N, 9°4′14.60″E) was collected in 2009 with a gravity corer in the Como Bay at a depth of 70 m. Half of the core was studied by Bettinetti *et al.* (2016) for DDT and PCB contamination assessment. The other half was kept for biological analysis. Independent dating was performed on each half of the core using radio-nuclides (Cesium activity in Bettinetti *et al.*, 2016, Cesium, Americium and Lead in the dating presented thereafter). We used the Constant Flux/Constant Sedimentation (CFCS) model and the decrease in $^{210}Pb_{ex}$ to calculate the sedimentation rates. The uncertainty of sedimentation rates obtained by this method was derived from the standard error of the linear regression of the CFCS model. Our chronology is highly consistent with the one published in Bettinetti *et al.* (2016).

The new dating performed by Pierre Sabatier at the LSM is presented thereafter in Figure 2.20, and indicate that the core covers the 1967-2009 period.

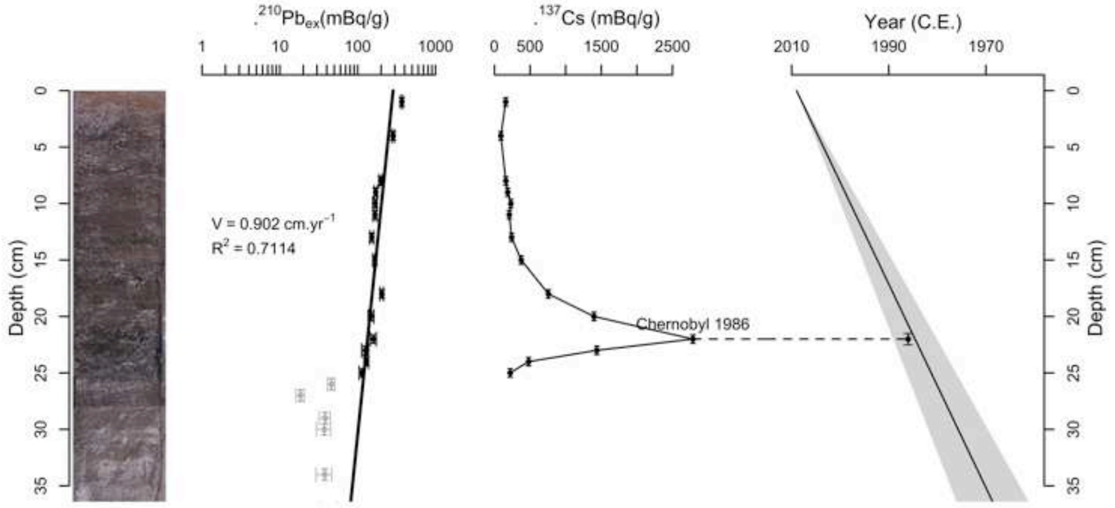


**Figure 2.20 I** Chronology for COMO09-02.

From left to right: photography, $^{210}Pb_{ex}$ activity, $^{137}Cs$ activity, and the age model for the 38 cm sequence. The $^{210}Pb_{ex}$ activity points in grey were not included in the sedimentation rate calculation because the low counting time was too low and led to large uncertainties at 1 σ. NWT stands for Nuclear Weapons Testing.

### 2.4.2 | LOCAL AND GLOBAL DRIVERS

Lake Como probably followed a similar eutrophication history that neighbouring lakes, but we do not have DI-TP to confirm it. However, monitoring data are available from 1973 and shows some maximum P concentration of 76 µg P.L$^{-1}$ (Figure 2.21), and a decrease of these concentrations from 1981 (Mosello *et al.*, 2010).

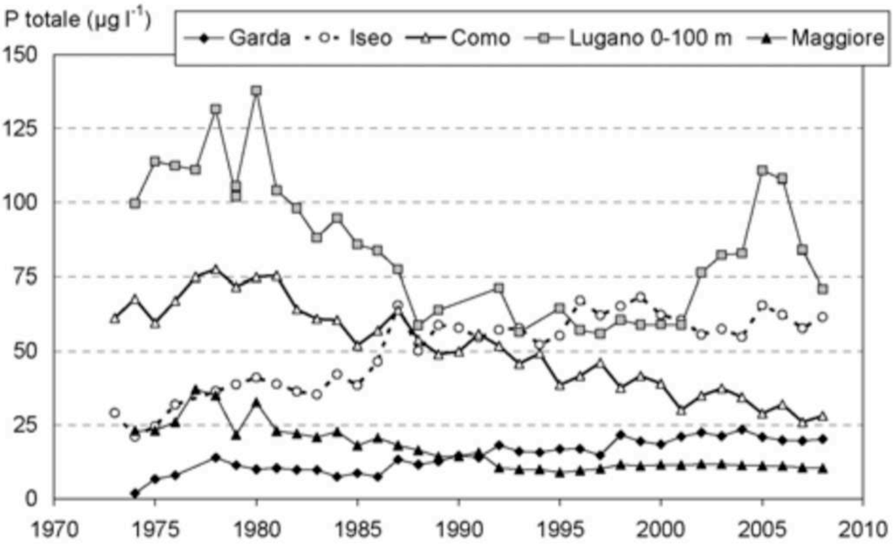


**Figure 2.21** I Evolution of total phosphorus concentrations during the spring circulation of Lakes Garda, Iseo, Como, Lugano and Maggiore.
(average concentrations on the water column at the point of maximum depth). For Lake of Lugano the average values of the layer between 0 and 100 m of depth have been considered. From Mosello *et al.* (2010).

### 2.4.3 | CLADOCERA

No transition in Lake Como cladoceran assemblage was observed for the 1967-2009 period. The community is largely gathers a diversity of pelagic grazers (all groups of *Bosmina* sp. as well as *Daphnia* spp.) but also some predators (*Leptodora kindti* and *Bythotrephes longismanus*). Some littoral species are also present, including the large *Sida crystallina*.

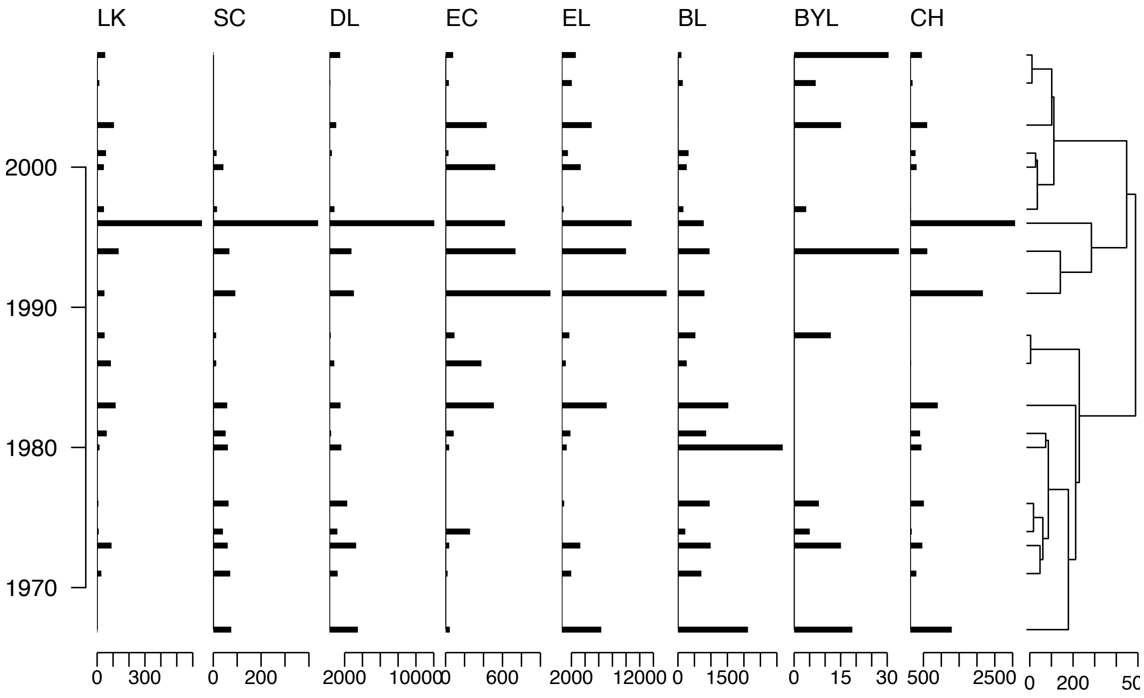


**Figure 2.22 I** Stratigraphic abundance of cladoceran remains in Lake Como sediment core COMO09-01. All littoral taxa were merged into a same groups, Chydoridae, to make the plot more readable. Abbreviations: BL= *Bosmina longirostris,* EC= *Eubosmina coregoni*, EL= *Eubosmina longispina*, DL= *Daphnia* spp., LK= *Leptodora kindti*, BYL= *Bythotrephes longismanus,* SC= *Sida crystallina*, CH= *Chydoridae*.

## 2.5 | LAKE GARDA AND LAKE LEDRO

Lake Garda, the largest Italian lake (Figure 2.23), and Lake Ledro, are the lakes located at the easternmost part of our study area, in Northern Italy. Similarly to the lakes at the South of the Alps barrier, these lakes present a high depth to surface ratio. Cores were taken and analysed to answer similar questions to those addressed in the IPER-RETRO program (for lakes Geneva, Annecy, Bourget) i.e. what are the responses of planktonic communities to the combined impacts of eutrophication and climate. Data were published in the framework of the PhD thesis of Manuela Milan.

### 2.5.1 | CORING AND DATING

Sediment samples were analysed for $^{210}$Pb, $^{226}$Ra, $^{137}$Cs and $^{241}$Am by direct gamma assay at ENSIS Ltd (University College London, UK), using an ORTEC HPGe GWL series well-type coaxial low background intrinsic germanium detector. As the use of the CIC (constant initial concentration) model was precluded due to the non-monotonic variations in unsupported 210Pb activity, core chronologies were calculated using the CRS (constant rate of $^{210}$Pb supply) dating model (Appleby, 2001).

### 2.5.2 | LOCAL AND GLOBAL DRIVERS

Trophic history was reconstructed using diatoms sub-fossils. These two lakes present a slightly later eutrophication than the occidental lakes in this study (Figure 2.24). Data on Lake Garda have been collected in the framework of the Long Term Ecological Research network (Lake Garda Station) and provided by FEM, S. Michele all'Adige.

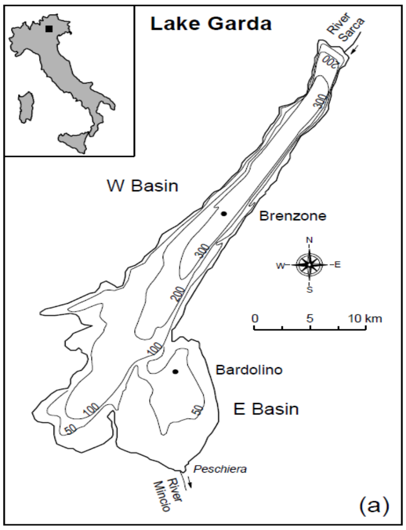


**Figure 2.23 I** Lake Garda with location of the two sampling points.
From Milan *et al.* (2017).

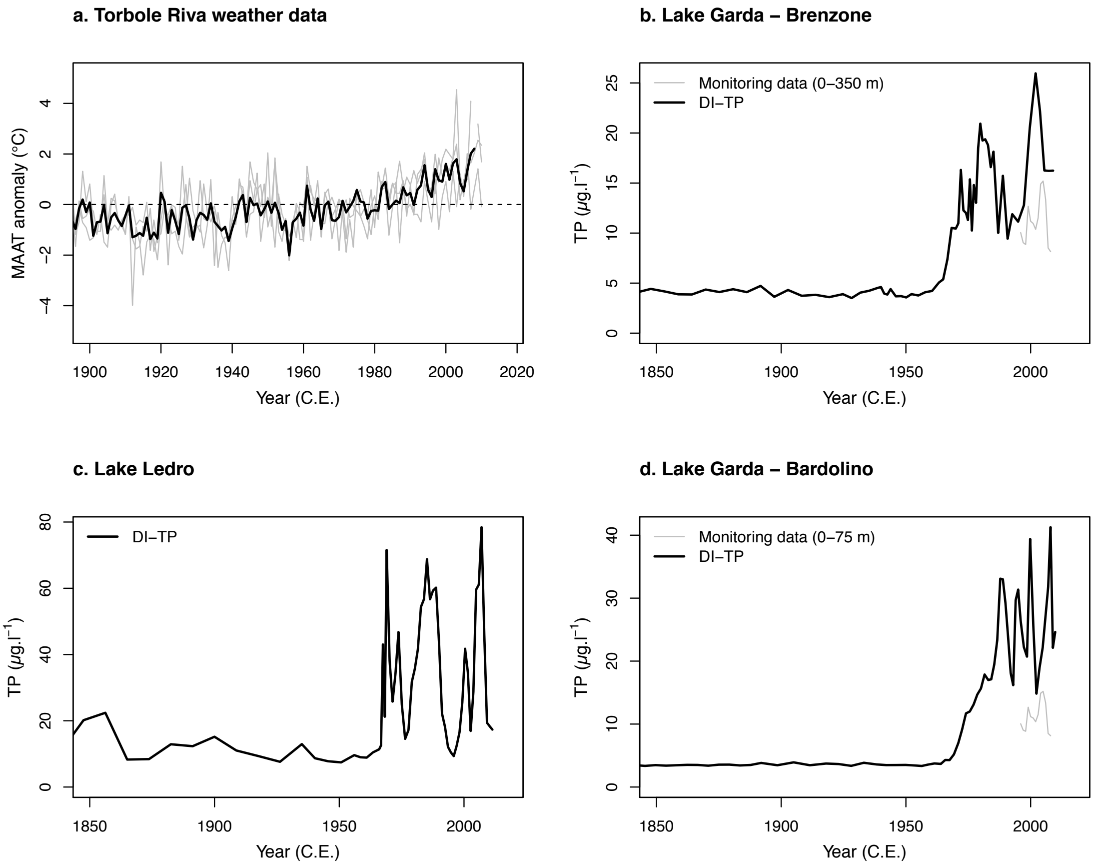


**Figure 2.24 I** Environmental data for Lakes Garda and Ledro.

(a) Weather data from Torbole Riva weather station, at the North of Lake Garda (East of Lake Ledro) (Auer *et al.*, 2007). Grey lines show seasonal temperature anomalies and black line shows the mean annual air temperature (MAAT) anomaly. (b, c, d) Monitoring data (grey line) and diatom-inferred total phosphorus (DI-TP, black line) for Lakes Garda (Brenzone basin), Lake Ledro and Lake Garda (Bardolino basin).

## 2.5.3 | CLADOCERA

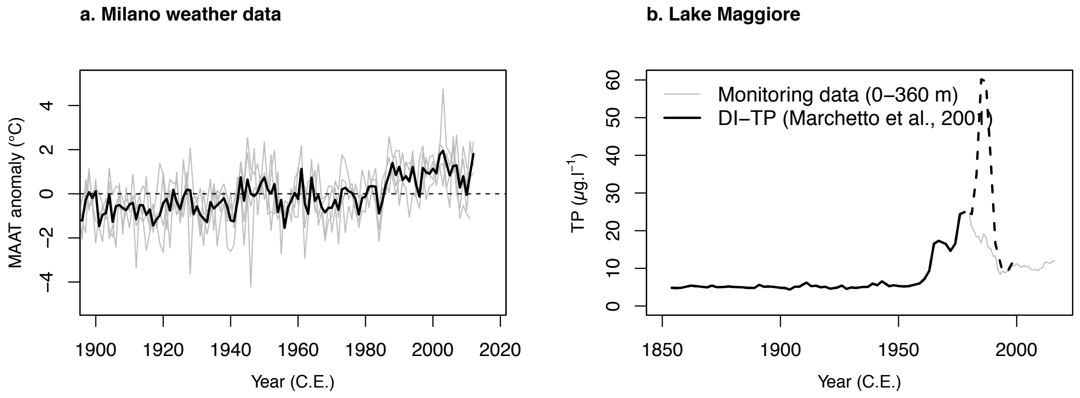
Cladoceran profiles are published in Milan *et al.* (2016; 2017)

## 2.6 | LAKE MAGGIORE

Lake Maggiore is the second largest (212 km$^2$) and deepest (370 m) Italian lake after Lake Garda (see 2.5 | above). It is one of the most well investigated lakes in Europe (de Bernardi *et al.*, 1990; Marchetto *et al.*, 2004; Manca *et al.*, 2007).

### 2.6.1 | CORING AND DATING

A 34 cm core was sampled in 2010 in Lake Maggiore (45°54.76'N, 8°32.96'E, z= 98 m) as part as a collaboration between Liisa Nevalainen, Meghan Brown, and Marina Manca. The chronology of the sediment sequence is based on the measurement of $^{137}$Cs activity carried out at University of Applied Sciences (Holland). It provided to anchoring point i.e. Chernobyl catastrophe in 1986 (14 cm) and the nuclear weapons test in 1963 (25 cm). Then a CFCS model was applied to interpolate the ages between these two anchoring points. The model is published in Nevalainen, Brown & Manca (2018).



**a. Milano weather data**

**b. Lake Maggiore**

**Figure 2.25 I** Environmental data for Lake Maggiore.

(a) Weather data from Milano weather station (Auer *et al.*, 2007). Grey lines show seasonal temperature anomalies and black line shows the mean annual air temperature (MAAT) anomaly. (b) Monitoring data (grey line) and diatom-inferred total phosphorus (DI-TP, black line) for Lake Maggiore. Black dashed line represent the unused DI-TP as monitoring data did not support such eutrophication.

### 2.6.2 | LOCAL AND GLOBAL DRIVERS

The lake is naturally oligotrophic (Guilizzoni *et al.*, 1983), but entered a mesoeutrophic state by the end of the 1960s as a consequence of the post-war economic development. The phosphorus load continued to increase until 1979 when measures were undertaken to reduce phosphorus loads to the lake. Monitoring data document the re-oligotrophication process (Figure 2.25), and TP was reconstructed from diatoms assemblage for the preceding period (Marchetto & Musazzi, 2001; Marchetto *et al.*, 2004). DI-TP reaches high-level in the late 1980s. This pattern is not supported by the monitoring data. The transfer function uses Wunsam & Schmidt (1995) training dataset, which may then overestimate enrichment levels. Similarly to our choice for Lake Geneva, we used a composite TP record, relying on DI-TP until 1979 and then switching to monitoring data from 1980. Long-term data on Lake Maggiore has been provided by the CNR ISE. These data have been collected trough the limnological campaigns funded by the International Commission for the Protection of Swiss-Italian Waters (CIPAIS).

### 2.6.3 | CLADOCERA

CONISS clustering identified three major periods based on the cladoceran composition (Figure 2.26). A high proportion of littoral taxa associated to macrophytic habitats characterizes the first period, from the beginning of the record in ca. 1944 until 1957. Many large species are represented (*Sida crystallina*, *Acroperus harpae*). Littoral species with less exigent requirements were also present, including large (*Alona affinis, Alona quadrangularis*) and smaller (*Alona guttata, Monospilus dispar, Paralona pigra*) species. In the pelagic area, both medium sized grazers (*Eubosmina longispina, Daphnia* spp.) and small grazers (*Bosmina longirostris*) share the habitat with the large predator *Leptodora kindti)*. The second period, between 1958 and 1973 is characterized by the loss of *Sida crystallina* and *Daphnia* spp., as well as the appearance of the large pelagic grazer *Eubosmina coregoni.* Since 1976, the pelagic assemblage is dominated by *E. longispina*, and *Chydoridae* diversity and abundance collapsed. A more detailed analysis is published in Nevalainen *et al.* (2018).

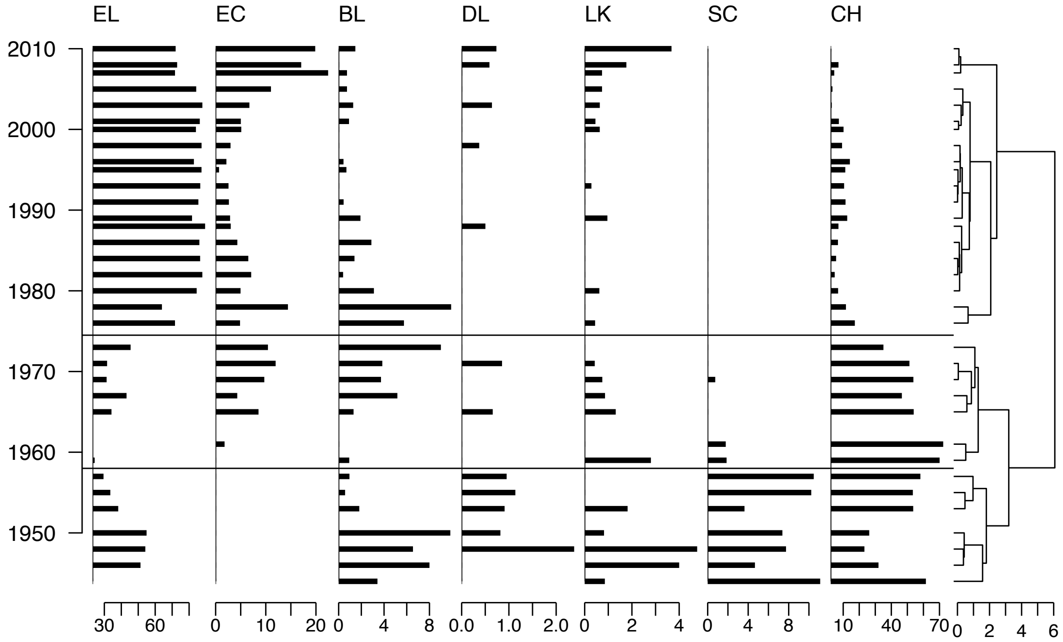


**Figure 2.26 I** Stratigraphic abundance of cladoceran remains in Lake Maggiore sediment core.

All littoral taxa were merged into a same groups, Chydoridae, to make the plot more readable. Abbreviations: BL= *Bosmina longirostris,* EC= *Eubosmina coregoni*, EL= *Eubosmina* *longispina*, DL= *Daphnia* spp., LK= *Leptodora kindti*, BYL= *Bythotrephes longismanus,* SC= *Sida crystallina*, CH= *Chydoridae*.

## 2.7 | LAKE LUGANO

Lake Lugano (271 m a.s.l.) has an average depth of 134 m, a water surface area of ca. 48.7 km$^2$ and a watershed area of ca. 565.6 km$^2$. The lake, at the border between Switzerland and Italy, displays a complex shape composed by three basins separated by two narrowings. The Vedeggio, Cassarate and Magliasina rivers mainly feed the lake. The Stresa river, flowing out from the Westernmost, smallest basin, is the main outlet.

### 2.7.1 | CORING AND DATING

We worked on a 139-cm-long core (LU-ME-11-1) sampled at the Melide station. The chronology of the Lake Lugano sediment sequence is based short-lived radionuclide measurements ($^{210}Pb_{ex}$ and $^{137}Cs$) to date the latest century. Short-lived radionuclide were measured on the top of the sediment sequence at the Modane Underground Laboratory (LSM) by gamma spectrometry, using high-efficiency, very low-back- ground, well-type Ge detectors (Reyss *et al.*, 1995). Then, we used the Constant Flux/Constant Sedimentation (CFCS) model and the decrease in $^{210}Pb_{ex}$ to calculate the sedimentation rates. The uncertainty of sedimentation rates obtained by this method was derived from the standard error of the linear regression of the CFCS model.

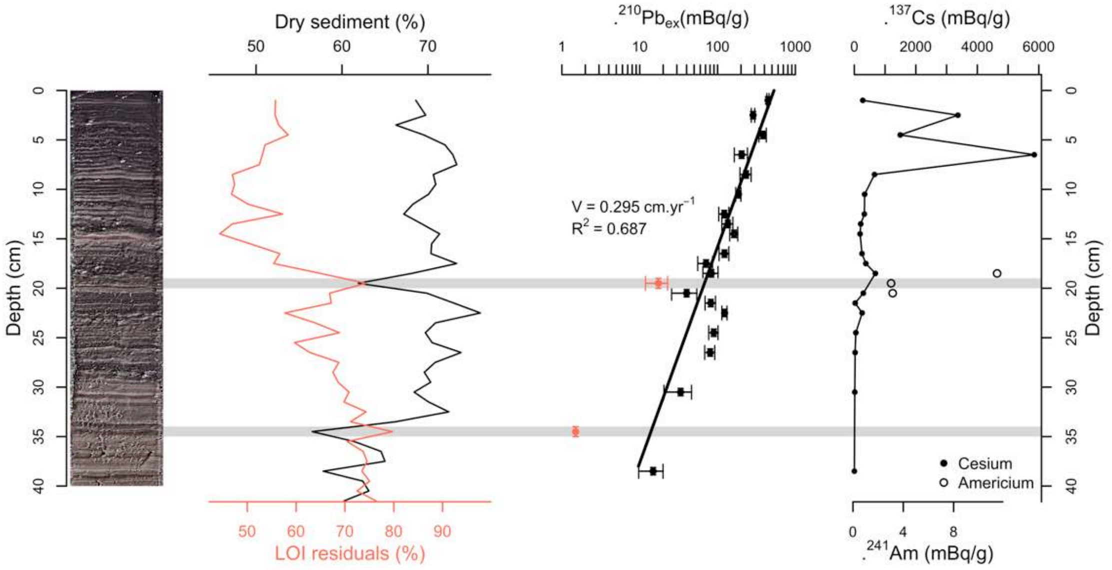


**Figure 2.27 I** Identification of event layers in LUME11-11.

From left to right: photography, dry sediment and LOI residuals proportion in samples (%), $^{210}Pb_{ex}$ activity, $^{137}Cs$ activity and $^{241}Am$ activity. The horizontal grey lines indicate layers that are considered as instantaneous events (higher LOI residuals, lower dry weight, lower $^{210}Pb_{ex}$ hence lower atmospheric supply).

The CSCF model using all the data did not provide a good fit ($R^2$= 0.69). Two samples (19-20 cm and 34-35 cm) displayed a particularly low and off-trend $^{210}Pb_{ex}$ activity. These two points are associated with samples with lower dry weight and higher LOI residuals (Figure 2.27). Such characteristics may indicate instantaneous events. DW and LOI also fluctuate asynchronously for two other samples (13-14 cm and 24-25 cm), but they are not associated with lower atmospheric $^{210}Pb$. By removing the two first events, we obtain a much better fit ($R^2$= 0.86, V= 0.37 $cm.yr^{-1}$, Figure 2.28) while removing 4 samples increases the $R^2$ to 0.88 and indicate a lower sedimentation rate (V= 0.33 $cm.yr^{-1}$).

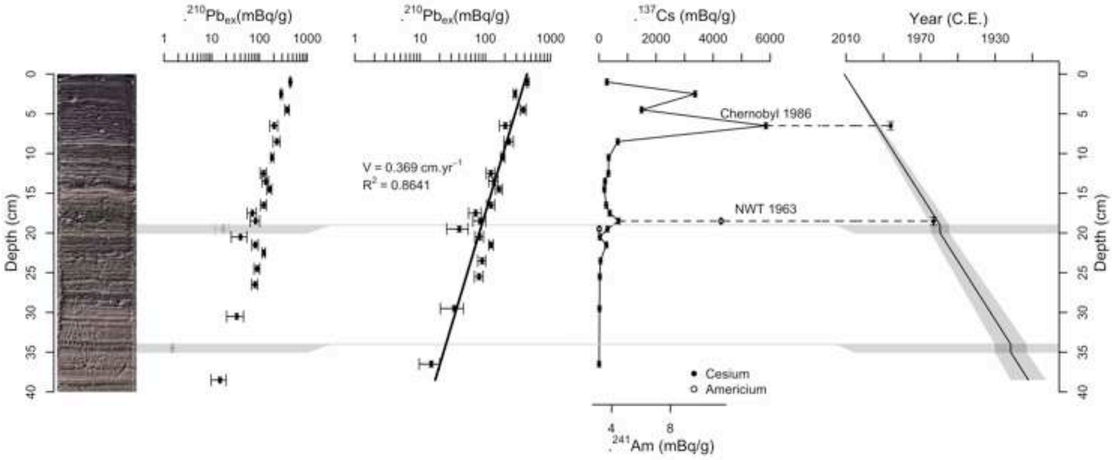


**Figure 2.28 I** Chronology for LUME11-11.

From left to right: photography, $^{210}Pb_{ex}$ activity with and without instantaneous deposit events, $^{137}Cs$ activity, and the age model for the 38 cm sequence. The $^{210}Pb_{ex}$ activity point in grey was not included in the sedimentation rate calculation. A change of sedimentation rate is revealed by $^{210}Pb_{ex}$ activity and identified by the change of color. NWT stands for Nuclear Weapons Testing.

### 2.7.2 | LOCAL AND GLOBAL DRIVERS

Lake Lugano history of perturbations is really well documented, with first reports dating back to the early 20th century (see Barbieri & Simona, 2001 for a synthesis). In the late 1970s, Ravera and Parise (1978) reconstructed the eutrophication process and its impact on the zooplankton communities using a palaeo-approach. Several cores taken in different part of the lake evidenced asynchronous changes in the basin.

Lake Lugano water quality has improved in the past decades, but nutrient levels are still high and the system remains eutrophic (Figure 2.29). However, the level given by DI-TP is significantly too high, as the TP concentration in the epilimnion is currently around 25 $\mu g.L^{-1}$

(70 µgTP.L$^{-1}$ in the whole water column). Data for Lake Lugano were collected for the CIPAIS monitoring programme (www.cipais.org) and were provided by F. Lepori at the Institute of Earth Sciences, SUPSI.

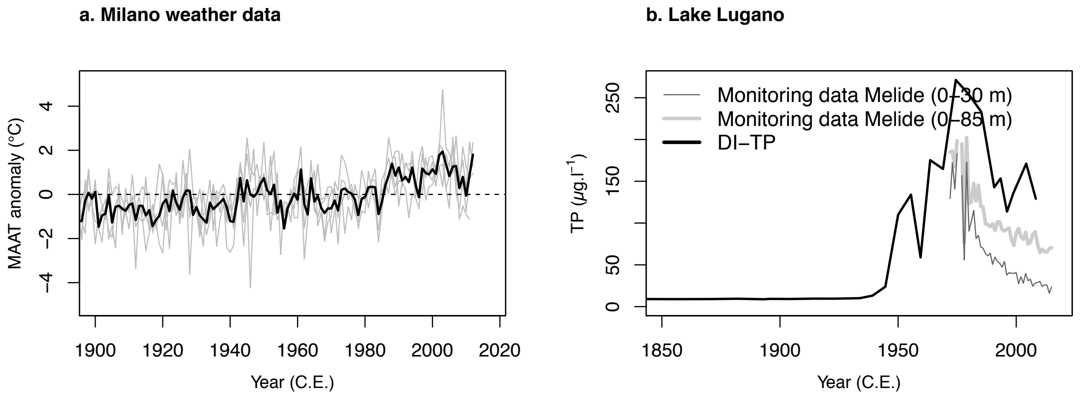


**Figure 2.29 I** Environmental data for Lake Lugano.

(a) Weather data from Milano weather station (Auer *et al.*, 2007). Grey lines show seasonal temperature anomalies and black line shows the mean annual air temperature (MAAT) anomaly. (b) Total phosphorus (TP) in Lake Lugano. Monitoring data (thick grey line: 0-85 m, thin grey line: 0-30 m) and diatom-inferred TP (DI-TP, black line).

### 2.7.3 | CLADOCERA

CONISS clustering identified three major periods based on the cladoceran composition (Figure 2.30). A high proportion of littoral taxa associated to macrophytic habitats characterizes the first period, from the beginning of the record in ca. 1638 until 1945. Both large (*Sida crystallina*, *Acroperus harpae*) and smaller (*Alonella nana, Alonella excisa*) taxa are represented. Littoral species with less exigent requirements were also present, with again a repartition between large (*Alona affinis, Alona quadrangularis*) and small (*Alona guttata, Monospilus dispar, Paralona pigra*) taxa. *Eubosmina longispina*, the earliest postglacial colonist in alpine lakes (Nauwerck, 1991), and *Daphnia* spp., dominate the pelagic assemblage. The second period, between 1950 and 1993 is characterized by the disappearance of *Sida crystallina*, followed a decade later by a loss of diversity and abundance of littoral taxa (*Chydoridae* family). The loss of the large littoral taxa was also reported by Ravera and Parise (1978). During this period, *Daphnia* spp. and *E. longispina* are replaced in the pelagic assemblage by the smaller grazer *Bosmina longirostris*. Finally, the recent-most assemblage since 1996 is characterized by a new shift between *B. longirostris* that disappear, and *Daphnia* spp. and *Eubosmina* sp. that recolonize the pelagic habitat of Lake Lugano. The pelagic predator *Leptodora kindti*, while present since the 19th century, is more abundant since the late 1980s and also showed a transient outbreak in the 1940s. Overall, our results compare well with those published by Ravera and Parise (1978). The insight they had on the spatial heterogeneity of assemblages in Lake Lugano prevents us from drawing conclusion to the whole lake. Instead, we shall consider the Melide basin as a distinct entity for which we will later evaluate the vulnerability to climate change.

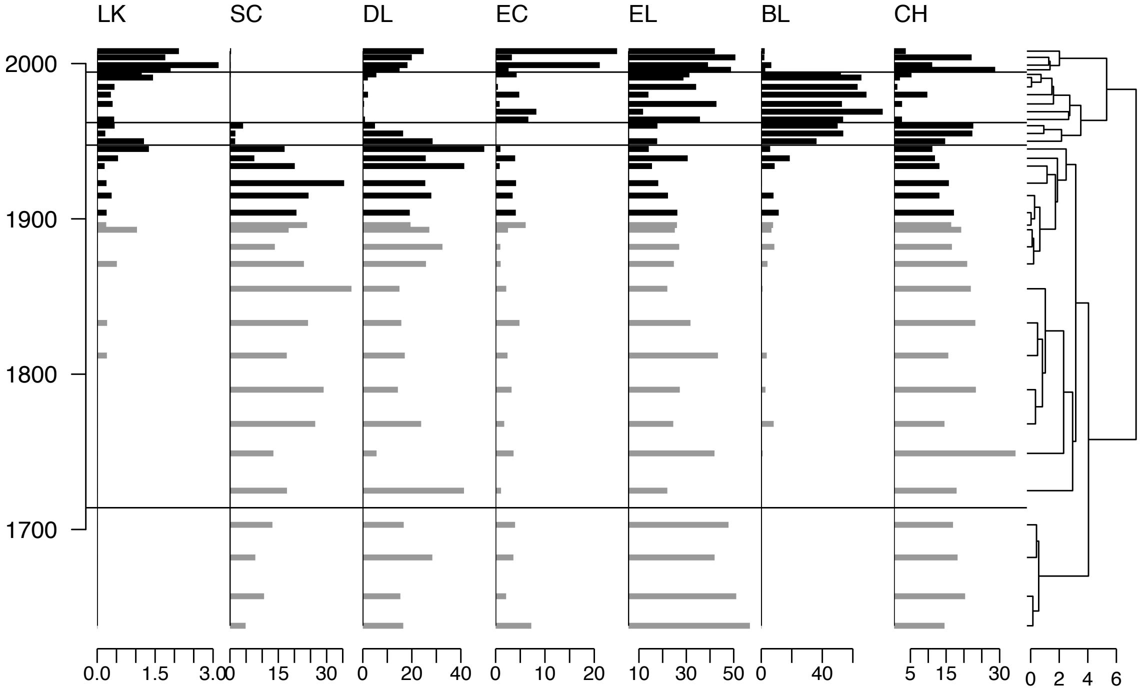


**Figure 2.30 I** Stratigraphic abundance of cladoceran remains in Lake Lugano sediment core LU-ME-11-1. All littoral taxa were merged into a same groups, Chydoridae, to make the plot more readable. Abbreviations: BL= *Bosmina longirostris,* EC= *Eubosmina coregoni*, EL= *Eubosmina longispina*, DL= *Daphnia* spp., LK= *Leptodora kindti*, BYL= *Bythotrephes longismanus,* SC= *Sida crystallina*, CH= *Chydoridae.* The black bars represent the sample >1900 and the grey bars represent the sample <1900

## 2.8 | LAKE JOUX

Lake Joux (1004 m a.s.l.) has a surface area of ca. 9 $km^2$ and a maximum depth of 31 m ($z_{mean}$= 22 m). The lake freezes almost every winter and the ice break-up occurs between March and the beginning of May. The lake is mainly fed by the meandering Orbe River, but also by several small streams located on the eastern shore. Lake Brenet and karstic caves are the main outlets of the lake, the latter becoming inlets during heavy rainfall events. The Orbe River re-emerges 3 km downstream of the lake. Lake Joux is the only lake that is not on the alpine bedrock, but instead part of the Swiss Jura Mountains.

### 2.8.1 | SEDIMENT CORING AND DATING

A 70-cm-long core was taken from the deep basin of Lake Joux in 2016 (JOU-16-02; 46.6399°N, 6.2875 °E). A previous 71-cm-long core (JOU-13-02; 46.6399°N, 6.2875°E) had been sampled in 2013 and dated using radiocarbon and radionuclides methods (Lavrieux *et al.*, 2017). Non-destructive magnetic susceptibility measurements were performed on both cores using a Geotek Multi-Sensor Core Logger (resolution: 5 mm), allowing the correlation between the two cores. The depth correlations are found in Table 2.5. Using a linear interpolation between the different points, the dated horizons of JOU-13-02 were projected onto JOU-16-02 (Table 2.6). We then calculated a continuous age-depth relationship with the R-code package 'Clam' version 2.2 (Blaauw, 2010b). JOU-16-02 record covers the past millennium (967-2016).

Figure 2.31 summarizes the different steps i.e. (1) correlation of magnetic susceptibility peaks (Figure 2.31 b), (2) dated horizons translated onto new cores, and (3) new age model computation (Figure 2.31 c).

The biological analyses were carried out on JOU-16-02 that was subsampled continuously every centimetre.

**Table 2.5 I** Depth correlation between the reference core JOU-13-02 (Lavrieux *et al.*, 2017) and JOU-16-02 (this study).

| Notable depths on JOU-13-02 (cm) | Corresponding depths on JOU-16-02 (cm) |
|---|---|
| 11 | 9.5 |
| 20 | 16.5 |
| 31 | 27 |
| 40 | 39.5 |
| 49 | 51 |
| 53 | 53.5 |
| 57 | 57 |
| 60.5 | 61.5 |

**Table 2.6 |** Dated horizons on JOU-13-02 and corresponding ages (Lavrieux *et al.*, 2017). The last column indicates the corresponding depth on JOU-16-02 of the dated horizons.

| Dated depth JOU-13-02 (cm) | Method | Age (AD) | Corresponding depth on JOU-16-02 (cm) |
|---|---|---|---|
| 9.5 | Radionuclide | 1963 | 8.2 |
| 15.5 | Radionuclide | 1950 | 13 |
| 18 | Radionuclide | 1936 | 14.9 |
| 22.5 | Radiocarbon | 1805 | 18.9 |
| 23 | Radiocarbon | 1791 | 19.4 |
| 24 | Radiocarbon | 1771 | 20.3 |
| 31.5 | Radiocarbon | 1639 | 27.7 |
| 42.5 | Radiocarbon | 1495 | 42.7 |
| 44.5 | Radiocarbon | 1455 | 45.3 |
| 47.5 | Radiocarbon | 1428 | 40.1 |
| 48.5 | Radiocarbon | 1415 | 50.4 |
| 56.5 | Radiocarbon | 1203 | 56.6 |
| 62.5 | Radiocarbon | 1110 | 64.1 |

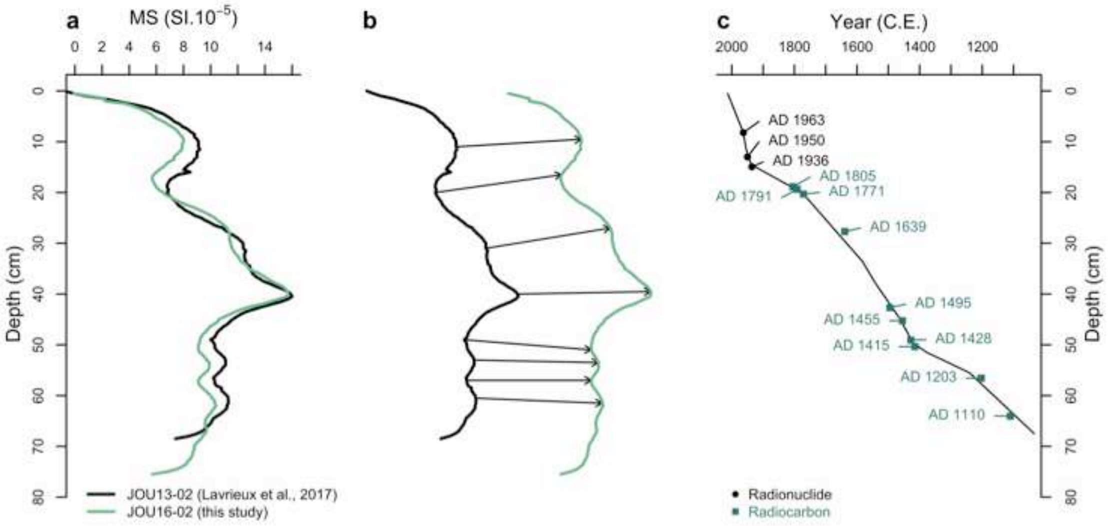


**Figure 2.31 |** Magnetic Susceptibility correlation in Lake Joux work and reference cores. (a) Magnetic Susceptibility (MS) of the reference core JOU-13-02 (Lavrieux *et al.*, 2017) and JOU-16-02 (this study). (b) Correlation between remarkable points. (c) Age-depth model for JOU-16-02.

## 2.8.2 | LOCAL AND GLOBAL DRIVERS

Lake Joux is located less than 30 km North from Lake Geneva, hence under the same climate for the past century. Lake Joux watershed (ca. 211 km$^2$) has a rather unusual history of human occupation, characterized by tardive but extensive settlement since the Late Middle Ages, followed by an intensive period of industrial development. This long history of impact was traced back by Lavrieux *et al.* (2017).

The first monitoring data in the 1980s suggest an eutrophic state during this period (25-35 µgP.L$^{-1}$, Figure 2.32) No data on the nutrient level are available before the 1980s, but macroscopic observations (development of *Planktothrix*) suggest that higher levels may have been reached in the second half of the 20th century (Fiaux *et al.*, 2006). 97% of the population on the watershed are now connected to one of the four wastewater treatment plants, respectively built in 1965, 1969, 1973 and 1993. Since the 2000s, phosphorus levels oscillate around 15 µgP.L$^{-1}$.

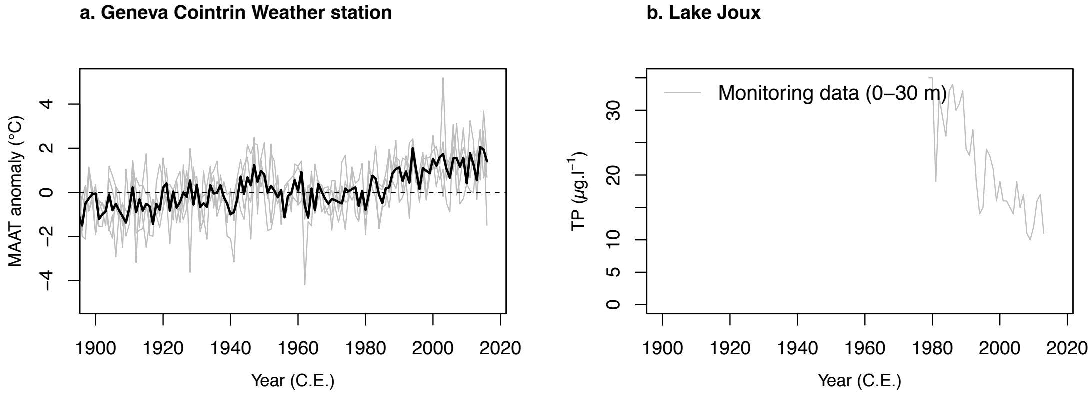


**Figure 2.32 I** Environmental data for Lake Joux.

(a) Weather data from Geneva Cointrin station. Grey lines show seasonal temperature anomalies and black line shows the mean annual air temperature (MAAT) anomaly. (b) Lake Joux total phosphorus (monitoring data, BAFU, 2016).

The lake was not only modified chemically but physically since the construction of a dam between the Joux and Brenet lakes in 1903. New works on the dam were carried out in 1943 in order to get a differential water level between the two lakes. These two modifications influenced the sedimentation and water dynamics of the lake, as well as the autochthonous communities of macrophytes and ostracods (Whittle, 2006).

Finally, human manipulated fish populations since at least the 13th century when monk established in the area introduced pike. From 1911 and 1931 respectively, artic char and whitefish were also introduced. Fish survey populations in the early 2000s reported the presence of 12 fish species in the lake and its inlets.

### 2.8.3 | CLADOCERA

CONISS clustering reveals 2 major groups with a transition between 1938 and 1954 (Figure 2.33). This period corresponds to the renovation of the dam between lakes Joux and Brenet, but also the period during which whitefish was introduced. The apparition of the large pelagic grazer *Eubosmina coregoni* and the disappearance of the large littoral group *Eurycercus* sp mark this transition. The later lives in macrophytic beds, and although it can migrate in the sediment in presence of fish, it is highly vulnerable to fish predation due to its size (Beklioglu & Jeppesen, 1999). While not significant in the CONISS clustering, two other successions can be observed in the pelagic. In the past 50 years, *Leptodora kindti* replacing *Bythotrephes longismanus* could mark a response to climatic forcings as those two species have similar ecology (pelagic predator), but *L. kindti* thrives in warmer waters.

Several other biological proxy were analysed from the core (photopigments, cyanobacterial DNA, chironomids, fish macroremains) as part as a research question led by Marie-Eve Monchamp and Nathalie Dubois at the EAWAG (Zürich) (see Abstract in Appendix 1: collaborations, p297).

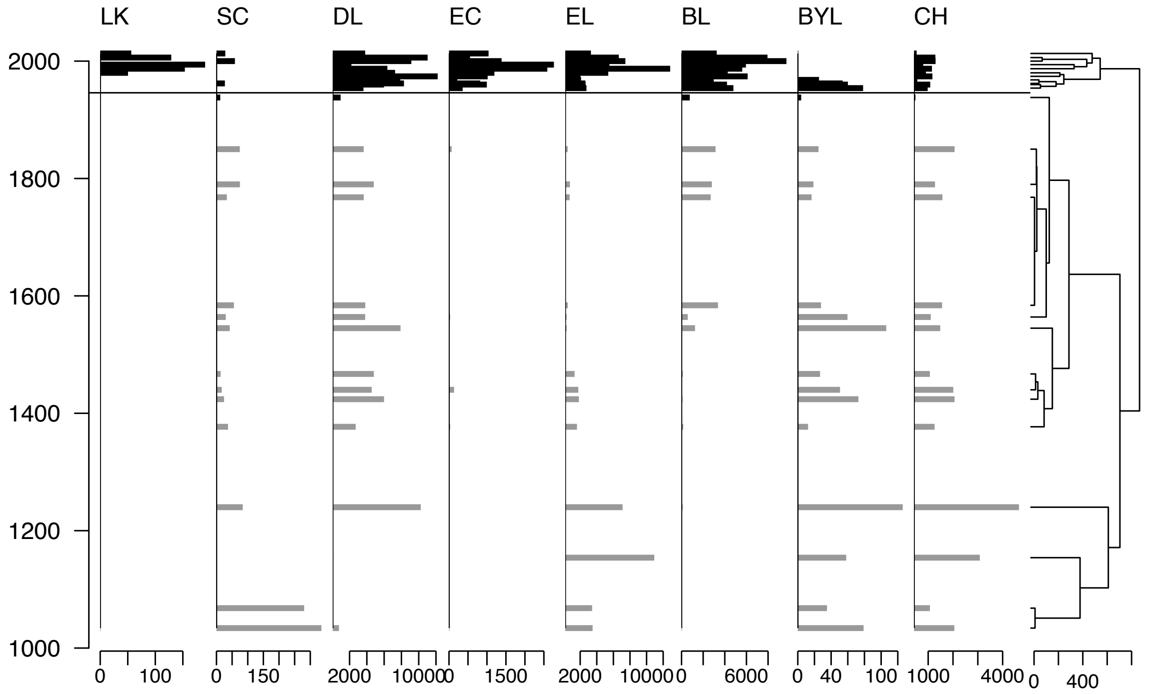


**Figure 2.33 I** Stratigraphic abundance of cladoceran remains in Lake Joux sediment core JOU16-02. All littoral taxa were merged into a same groups, Chydoridae, to make the plot more readable. Abbreviations: BL= *Bosmina longirostris,* EC= *Eubosmina coregoni*, EL= *Eubosmina longispina*, DL= *Daphnia* spp., LK= *Leptodora kindti*, BYL= *Bythotrephes longismanus,* SC= *Sida crystallina*, CH= *Chydoridae*. The black bars represent the sample >1900 and the grey bars represent the sample <1900.

## 2.9 | LAKE ZÜRICH

Lake Zürich is the northernmost lake in the study. It has a surface area of 65 $km^2$ and a maximum depth of 136 meters. The lake is divided into two basins. The lake is considered to be monomictic or dimictic, but the increase of strength of thermal stratification in the last few decades as a consequence of climate warming impedes complete mixing of the water column (Anneville *et al.*, 2004).

### 2.9.1 | CORING AND DATING

A short core (ZH-17-21, 103 cm) was taken from the pelagic zone in 2017. Only the upper 50 cm were sampled and analysed within this study. The sediment of Lake Zurich presents a laminated facies on the surface (0-28.3 cm) that allowed varves counting (Figure 2.34). A linear interpolation allowed getting ages for the rest of the core. There was no change of sedimentation for the top 22.5-cm (1930-2017) which support the realism of such approximation. From 22.5 cm downward, the model fitted with only 3 points indicates a higher sedimentation rate.

The sediment sequence covers the 1945-2017 period. The core was subsampled every centimetre for biological analysis (diatoms and cladocera remains).

### 2.9.2 | LOCAL AND GLOBAL STRESSORS

Lake Zürich went from an oligotrophic to a eutrophic state in the past 120 years. The population on its watershed increased rapidly and early in its history compared to French and Italian lakes. Indeed, Boucherle & Züllig (1983) report an increase in population of +240% between 1850 and 1980. The adoption in 1871 of slow sand filters to treat drinking water pumped from the lake come as an early indicator of change in water quality. Moreover, in 1895, Lake Zürich sediments became annually laminated (Nipkow, 1920), which suggest the appearance of deep-water anoxia (Jenny *et al.*, 2016).

TP levels were reconstructed from the diatoms assemblage and support the timing of eutrophication proposed by Boucherle & Züllig (1983) i.e. degradation of water quality from the late 1900th century and short-lasting increased water quality in the early 1940s (Figure 2.35).

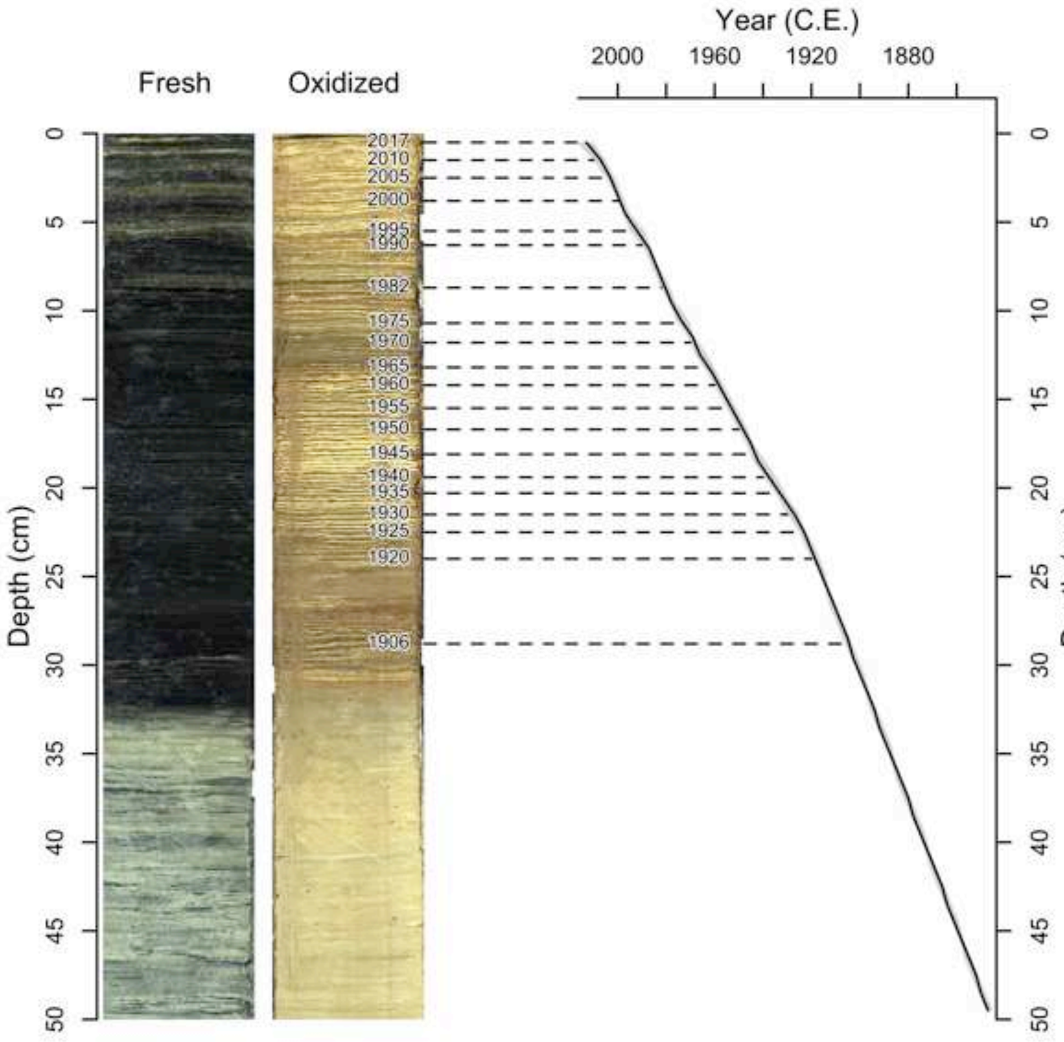
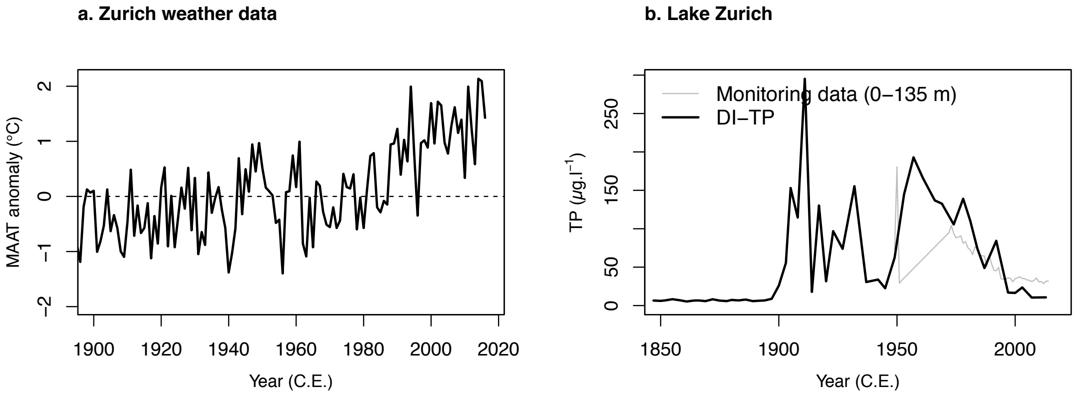


**Figure 2.34 l** Varves counting and age model for Lake Zurich core ZH17-21.

From left to right: photography of fresh and oxidised sediment, varve counting and age-depth model.


a. Zurich weather data

b. Lake Zurich

**Figure 2.35 l** Environmental data for Lake Zurich.

(a) Mean annual air temperature (MAAT) anomaly from Zurich weather station. (b) Monitoring data (0-135m, grey line) and diatom-inferred total phosphorus (DI-TP, black line).

### 2.9.3 | CLADOCERA

CONISS clustering identified four significant different cladoceran assemblages over the past 170 years. From 1845 to 1903, *Eubosmina longispina* and the predator *Bythotrephes longismanus* dominate the pelagic assemblage. macrophyte-associated species are present (*Eurycercus* sp*.*, *Alona quandrangularis*, *Sida crystallina*) attesting for the presence of macrophytic littoral zone. From 1905 to 1908, there is a transient assemblage dominated by pelagic taxa (*Daphnia longispina* and *Bosmina longirostris*). The later is a small taxa, wall the usually large *Daphnia longispina* lose 25 µm in average at this period (Figure 2.37). This smaller assemblage is associated with a transient disappearance of predator species (*Leptodora kindti*). This dynamic alone would require more investigation and may come from a change in the top-down pressure, if fish happened to be introduced at that time. However, I did not find any information in the English-written literature mentioning fisheries management of Lake Zurich at that time. The following period from 1911 to 1957 is characterized by a dominance of *Daphnia* spp. and *Bosmina longirostris* species in the pelagic compartment. The predator *B. longismanus and Leptodora kindti* are also present. The overall abundance of littoral taxa increases, but the macrophyte-associated taxa are replaced by more ubiquitous taxa (*Chydorus sphaericus*). The last transition took place from 1961, and characterise the recent assemblage. The overall abundance increases for almost all groups. Larger pelagic grazers returned (*Eubosmina* sp., larger size *Daphnia* spp. Figure 2.37). Large predators share the habitat. *Chydoridae* taxa remained an important part of the assemblage despite eutrophication, unlike what happened in many other lakes of the study.

Boucherle & Züllig (1983) used the shift between assemblages dominated by *Daphnia* spp. and *Bosmina* sp. to infer the level eutrophication. Using this ratio, we are in accordance with their results and timing of water quality. The insight brought from diatoms analysis on the trophic level also corroborates a two-stages eutrophication, with an increase in water quality in the early years of World War II. Globally, *Daphnia* spp. group is once again (Alric *et al.*, 2013) providing an early warning for eutrophication with their abundance increasing as soon as 1883.

Having said that, the identification to the specie level in the *Bosmina* sp. group differs between their study and the present sequence (Figure 2.36). We did observe the appearance of the small *Bosmina longirostris* group from the late 19th century, but found remains of *Eubosmina longispina* during the 20th century as well while Boucherle & Züllig (1983) reported its total disappearance from the sediment. Overall, the results are still very similar, and the difference may come from misidentifications or updated identification keys.

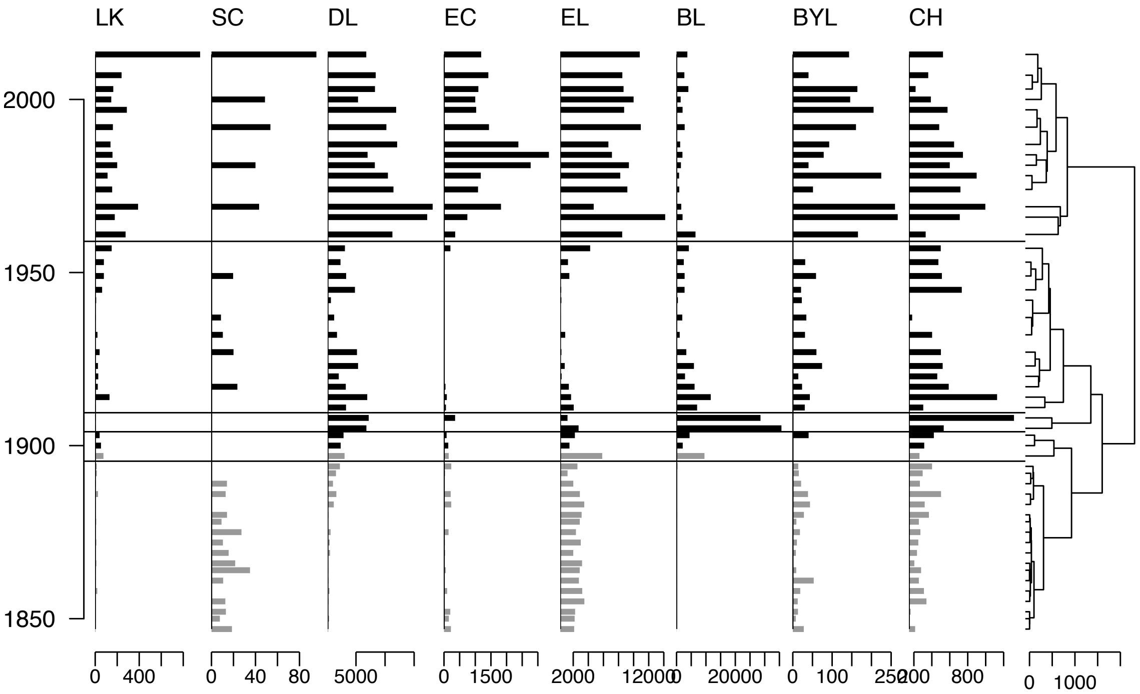


**Figure 2.36 I** Stratigraphic abundance of cladoceran remains in Lake Zürich sediment core ZH17-21.

All littoral taxa were merged into a same groups, Chydoridae, to make the plot more readable. Abbreviations: BL= *Bosmina longirostris,* EC= *Eubosmina coregoni*, EL= *Eubosmina longispina*, DL= *Daphnia* spp., LK= *Leptodora kindti*, BYL= *Bythotrephes longismanus,* SC= *Sida crystallina*, CH= *Chydoridae*. The black bars represent the sample >1900 and the grey bars represent the sample <1900.

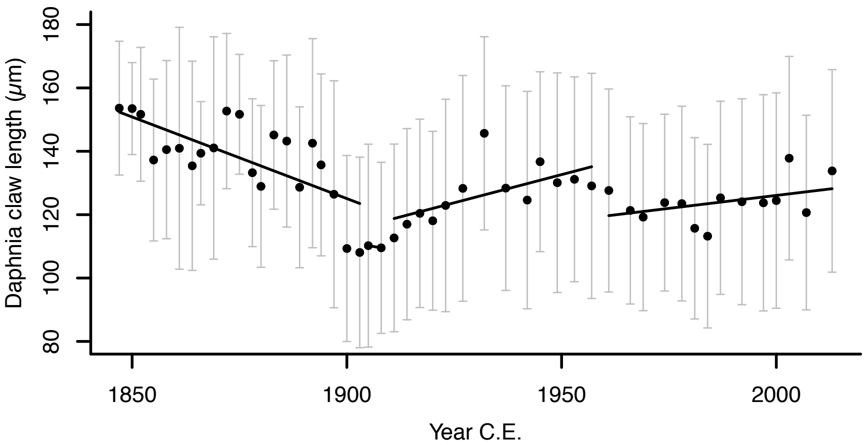


**Figure 2.37 I** Average Daphnia spp. claw size (*μ*m) in Lake Zurich sediment.

Grey bars indicate standard deviations, and black lines are average claw size for the 4 periods identified by the CONISS clustering.

## 2.10 | SYNTHESIS OF THE LAKES TRAJECTORIES

The assemblages of the twelve lakes consisted mostly of pelagic taxa, which were expected as all the cores were taken in the pelagic zone. The timing of significant transition varied among lakes (Figure 2.38), with lakes whose assemblage changed as soon as the late 19th century (e.g. Lakes Aiguebelette, Zurich), and other lakes that exhibit great stability until the mid-20th century (e.g. Lakes Bourget, Lugano). The great number of observations required ordination methods to identify the main trends in the assemblage. I present these methods in the following section.

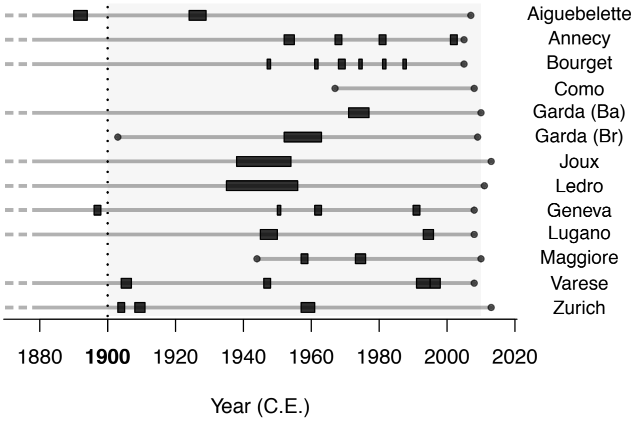


**Figure 2.38 I** Summary of the significant transitions in lakes assemblages as detected by CONISS clustering.

Grey horizontal lines depict the periods covered by each record (name of the lakes on the right), dots indicate first and last sample (dotted grey lines indicate that the records started before 1870). The black rectangles identify for each records the range of time during which major transitions took place. Slacker sampling resulted in larger incertitude for the transition (e.g. in Lakes Joux and Ledro, 1940s-transitions).

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# Chapter | 3

# Results of the investigations on potential statistical tools

# 3 | RESULTS OF THE INVESTIGATION ON POTENTIAL STATISTICAL TOOLS

This chapter introduces the main statistical methods used thereafter. It also represents an occasion of presenting some limitations of the methods. Data aggregation and statistical analyses were performed using R version 3.1.2 (2014-10-31, R Core Team, 2014), as well as the packages cited below.

## 3.1 | INTRODUCTION TO THE MAIN STATISTICAL TOOLS

### 3.1.1 | ORDINATION METHOD

The data we are working on after the analytical phase are multivariate i.e. each observation (year) is characterized by several variables (species). For example, in Figure 3.1, the 1940-assemblage is composed of one *Daphnia* spp., five *Eubosmina longispina,* one *Paralona pigra* and two *Acroperus harpae*. From this really small subset it is possible to tell that the assemblages of 1940 and 2000 are more alike than the 1970-one because only relative abundances change. On the other hand, *Daphnia* spp. dominates the 1970-assemblage, and *A. harpae* disappeared. However, the same environmental conditions may be favouring *Daphnia* spp. and impacting *E. longispina* and *A. harpae*. The former taxa show asynchronous changes with the two later taxa. Recording the changes in these three species separately would boil down to identifying the same gradient, because these three variables (species) appear correlated.

Ordination methods allow going beyond this qualitative description, and transforming multivariate data into univariate data, where similar observations will get the same scores. There are different methods including principal component analysis (PCA, Jolliffe, 1986), correspondence analysis (CA), and detrended correspondence analysis (DCA, Hill & Gauch, 1980). The difference lies in the construction of the axes. We compared several methods (see below) and explain here the main idea of ordination tools using PCA as a showcase. In practice, data are projected into a n-dimension cloud (where n is the total number of variables minus 1). Then, a first axis goes through this cloud with the objective to maximize the variance. With the variability left, a second axis goes through the cloud and explains more variance. This step is repeated until all the variability in the dataset is explained. The result is a new set of n dimension, each of them explaining gradually less variance as the variance is maximised in the first dimensions. There cannot be more dimensions than initial variable. The input data is sometimes transformed prior to computation to account for specificity of the initial data. For instance, the Hellinger transformation is particularly suited to species abundance data. This transformation gives low weights to variables with low counts and many zeros. The transformation itself comprises dividing each value in a data matrix by its row sum, and taking the square root of the quotient. Sometimes, it is arguable to give a low weight to species with low counts and many zeros because their presence can be highly indicative of a given phenomenon. Then, other transformations can be used, including the $X^2$ transformation. In this transformation, each value in a data matrix is divided by the product of its row sum with the square root of its column sum.

Coming back to our example, the PCA ran on the initial dataset allowed to identify only two dimensions. Those two dimensions are enough to describe the variability initially carried out by four descriptors (species), hence the frequent expression 'dimension reduction'. The first dimension (PC1, horizontal scores on Figure 3.1 a) discriminate 1970 (negative score) from 1940 and 2000 (positive scores). It supports the initial intuition that 1970 was the year with the most different assemblage. Besides, most of the variability in the dataset is explained on this axis (74%). Because the dataset is really small, the second dimension (PC2) explained the remaining variability i.e. the difference between 1940 (negative score on PC2 and 2000 (positive score on PC2).

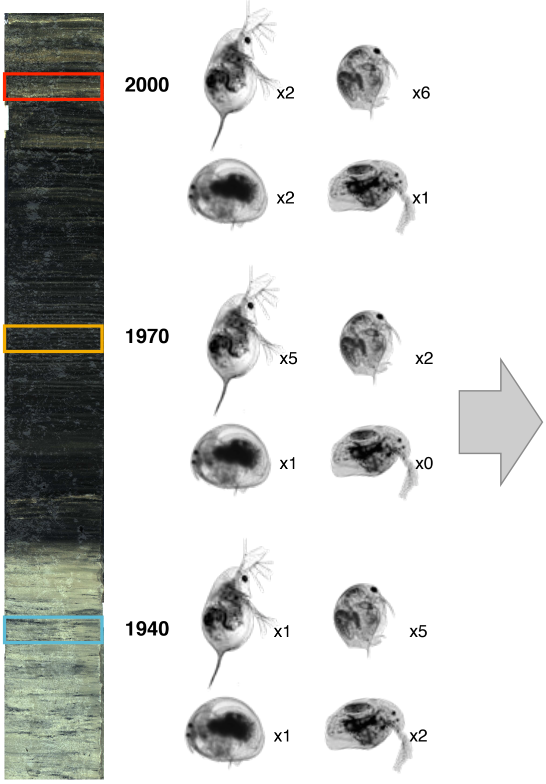
Each species contributes to the new dimensions, and PCA allows extracting this information. Indeed, species loadings on each axis quantify by which extent any specie is important to observations (years) that scored on that dimension. The initial feeling that *Daphnia* spp. changed asynchronously with *E. longispina* and *A. harpae* is comforted by the loadings on PC1 (Figure 3.1 b, middle graph). The former has negative loadings (and 1970 obtained a negative score on PC1), and conversely, the later have positive loadings. Regarding the variance on PC2, we learn that the 2000-assemblage is different from the 1940-assemblage mostly because *P. pigra* is twice as abundant in the former, and this is why *P. pigra* scores high on PC2 (Figure 3.1 b, right graph).

The method becomes particularly useful in larger datasets to extract dominant gradients (Figure 3.1 c). The basic hypothesis is that changes in the assemblage are driven by changes in the environment (any level considered, e.g. abiotic conditions, intra- or inter-specific competition). In other words, the two dimensions on our example should in fact reflect two gradients of environmental conditions.

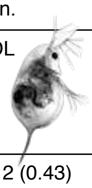
**Figure 3.1 I (next page ➔)** Principle of principal component analysis (PCA).

(a) Each observation (e.g. dated sediment sample) is characterized by a specific assemblage of Cladocera determined through microscopy. Species codes: DL= *Daphnia* spp., EL= *Eubosmina longispina*, PP= *Paralona pigra*, AH= *Acroperus harpae*. (b) PCA is run on the dataset and creates new independent dimension. For this simple example, two dimensions were enough to summarize the whole variability. Scores can be projected in 2D spaces (left) and the contributions of each species to each dimension can be extracted (two barplots). (c) New principal components can be used as independent variables.

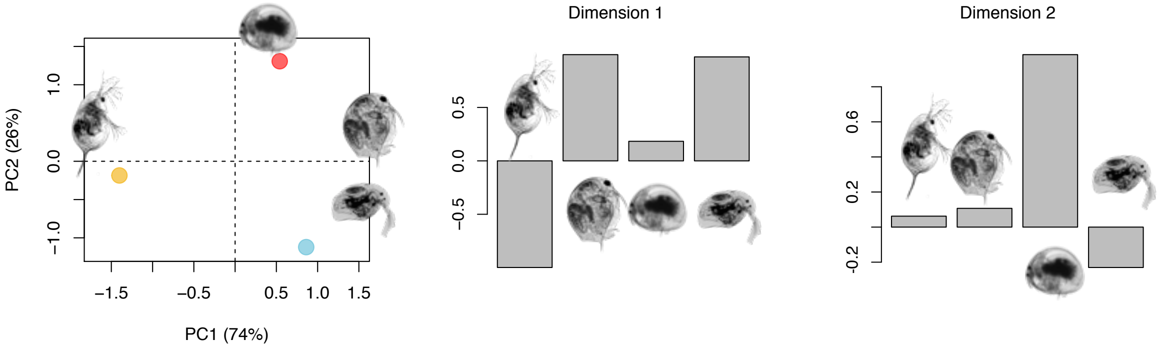
**a. Step 1:** Identification of cladoceran remains to infer past communities



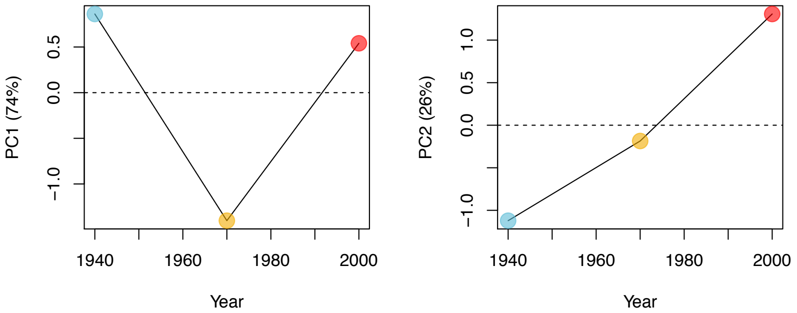
Faunistic list of cladoceran species (variables) by years (observations). Numbers in brackets are data after Hellinger transformation.

| | DL  | EL  | PP  | AH  |
|---|---|---|---|---|
| **2000** | 2 (0.43) | 6 (0.74) | 2 (0.43) | 1 (0.30) |
| **1970** | 5 (0.79) | 2 (0.50) | 1 (0.35) | 0 (0.00) |
| **1940** | 1 (0.33) | 5 (0.75) | 1 (0.33) | 2 (0.47) |

**b. Step 2:** PCA computation. Observations are projected in n dimensions. Species loadings on each axes inform on species relative contribution to the new dimensions.



**c. Step 3:** New independent dimensions describe the main variance in the assemblage



### 3.1.2 | General additive models

We used general additive models (GAM) to decipher the contribution of the two main stressors (climate warming and eutrophication) on the cladoceran assemblages dynamics (see Chapter 4 to 6 for application). The method is well explained in Simpson & Birks (2009). In short, the contribution of potential driver to a response variable is modelised including a smooth term (as Driver 1 in Figure 3.2). Other advantages of GAM over general linear models include the possibility to account for irregular sampling in the model through testing the contribution of auto-correlative structures (AR(1) and CAR(1)). We used GAM in the later analyses, but acknowledge its limitation i.e. it does not account for any potential bi-stability of responses over time.

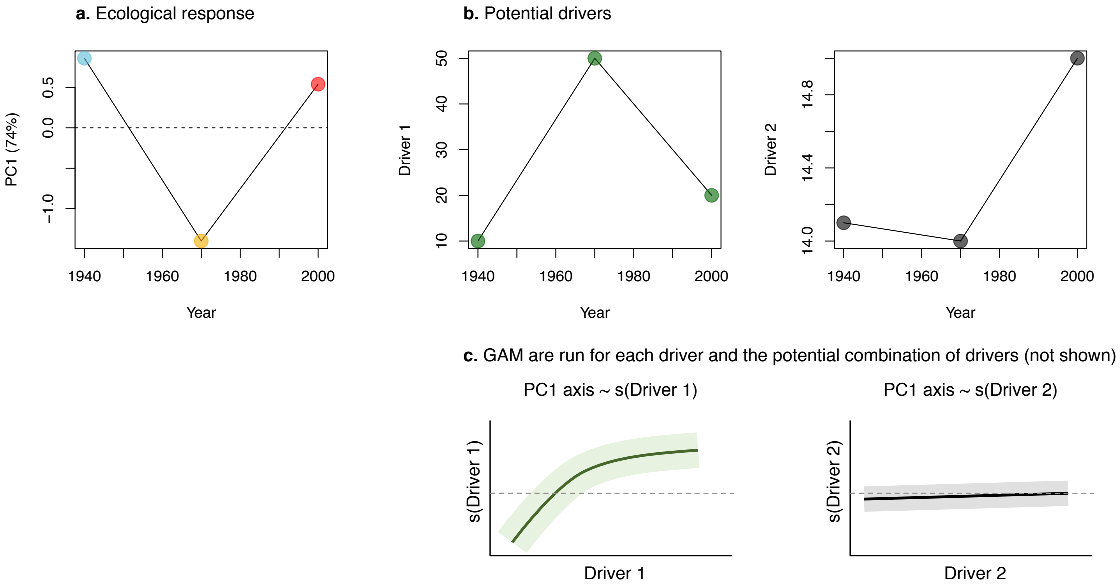


**Figure 3.2 I** Principle of general additive models (GAM).

Like other models, GAM is designed to explain a response variable (a) from potential drivers (b). GAM is a powerful method particularly fitted to ecological datasets as it allows including a smooth parameter, as in (c).

## 3.2 | EARLY WARNING SIGNALS

The theory beyond early warning signals (EWS) is introduced in Chapter 1 and applied in Chapter 4. This paragraph is a Supplementary Materials to the analysis carried out on Lake Varese (Bruel *et al.*, 2018).

Autocorrelation (AR(1)) and variance (SD) were used as EWS of catastrophic transitions in Chapter 4. These indicators are calculated from a selected window. They were generated under R (package "earlywarnings", Dakos *et al.*, 2012). Several window sizes were tested on Lake Varese data (Chapter 4) to understand the impact on the signals (Figure 3.3 to Figure 3.7). The trends were calculated relying on Mann-Kendall's rank correlation test (MK test). An MK test was chosen because the EWS are expected to result in monotonic trends. For small window sizes, the trend was not monotonic. The example of AR(1) computed on raw DCA1 indicates that, as the window size increases, the general trend always became positive (Figure 3.3). This is reflected in Figure 3.4, Figure 3.5, Figure 3.6, Figure 3.7, whereas AR(1) is always significantly positive (panels a, b, c) as the window size increases. Several window sizes were also used for MK test computation to obtain better insight. The results for different windows sizes (depicted by arrows in Figure 3.3) are found in Figure 3.4 (window= 6), Figure 3.5 (window= 8), Figure 3.6 (window= 10), and Figure 3.7 (window= 12). This indicates that there was no significant trend in (AR(1) before the 1926 / 1948 transition, whereas the increase in SD was reflected by all window sizes, despite the number of samples used for the MK test. The results for the 1946 / 1948 transition in the MK test computed in 10 (Figure 3.6 b, e, h, k) and 12 (Figure 3.7 b, e, h, k) samples had to be considered carefully as they include the previous transition. These results outline that for window size= 20, there is a trend in AR(1) and SD. The results for the 1983 / 1988 transition do not exhibit an increase in AR(1) and SD.

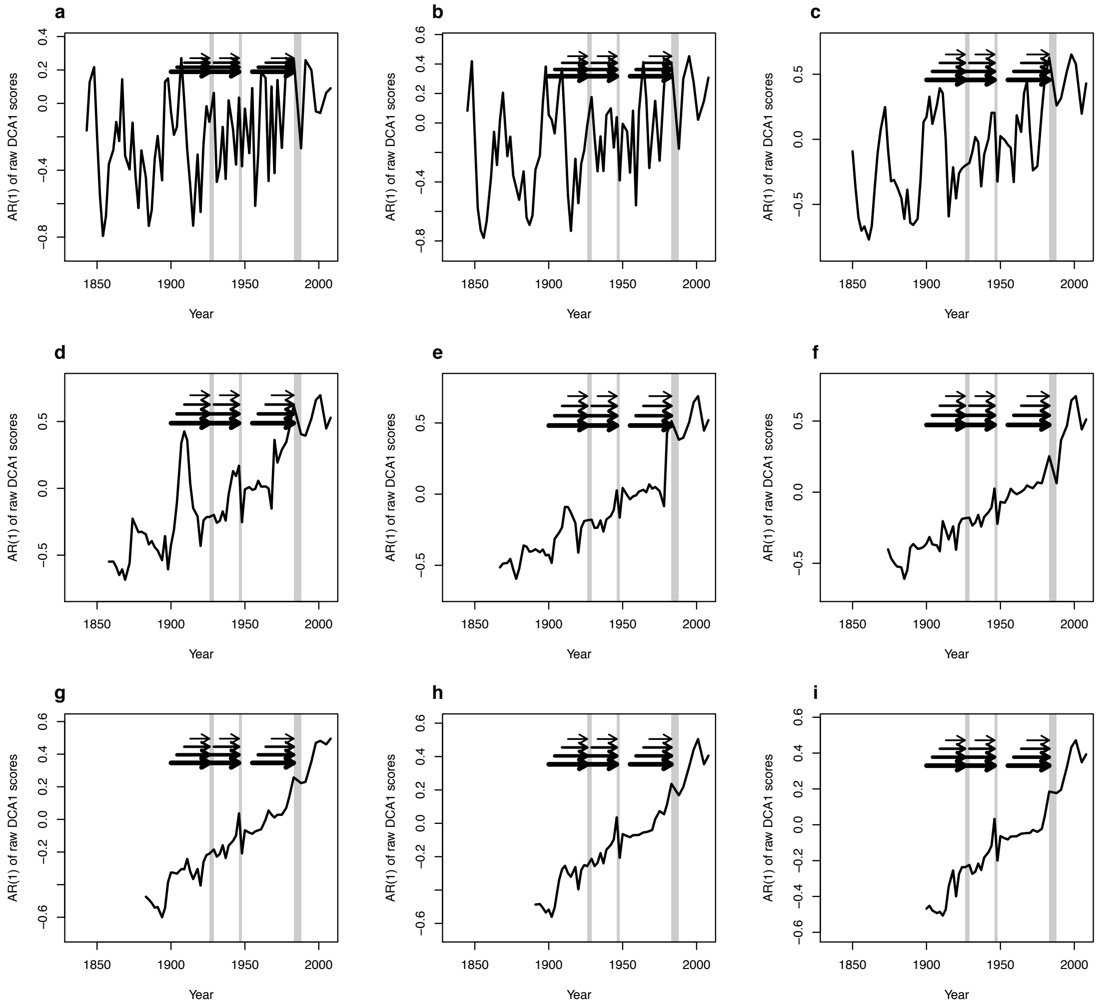


**Figure 3.3 I** Example of the impact of various window sizes (5 to 40) on the calculation of autocorrelation (AR(1), thick line) trend, an Early Warning Signal (EWS).

Window sizes represented here are (a) 5, (b) 7, (c) 10, (d) 15, (e) 20, (f), 25, (g) 30, (h) 35, (i) 40, in percentage of the length of the variable (DCA1 scores i.e. 74 samples). The trend in EWS was calculated by Mann Kendall' rank correlation test for A:B windows with A= break and B= sample number before break. Arrows represents the different windows used to calculate the trend in autocorrelation (trend calculated for B= 6, B= 8, B= 10, B= 12, from thinnest to thickest arrow, respectively).

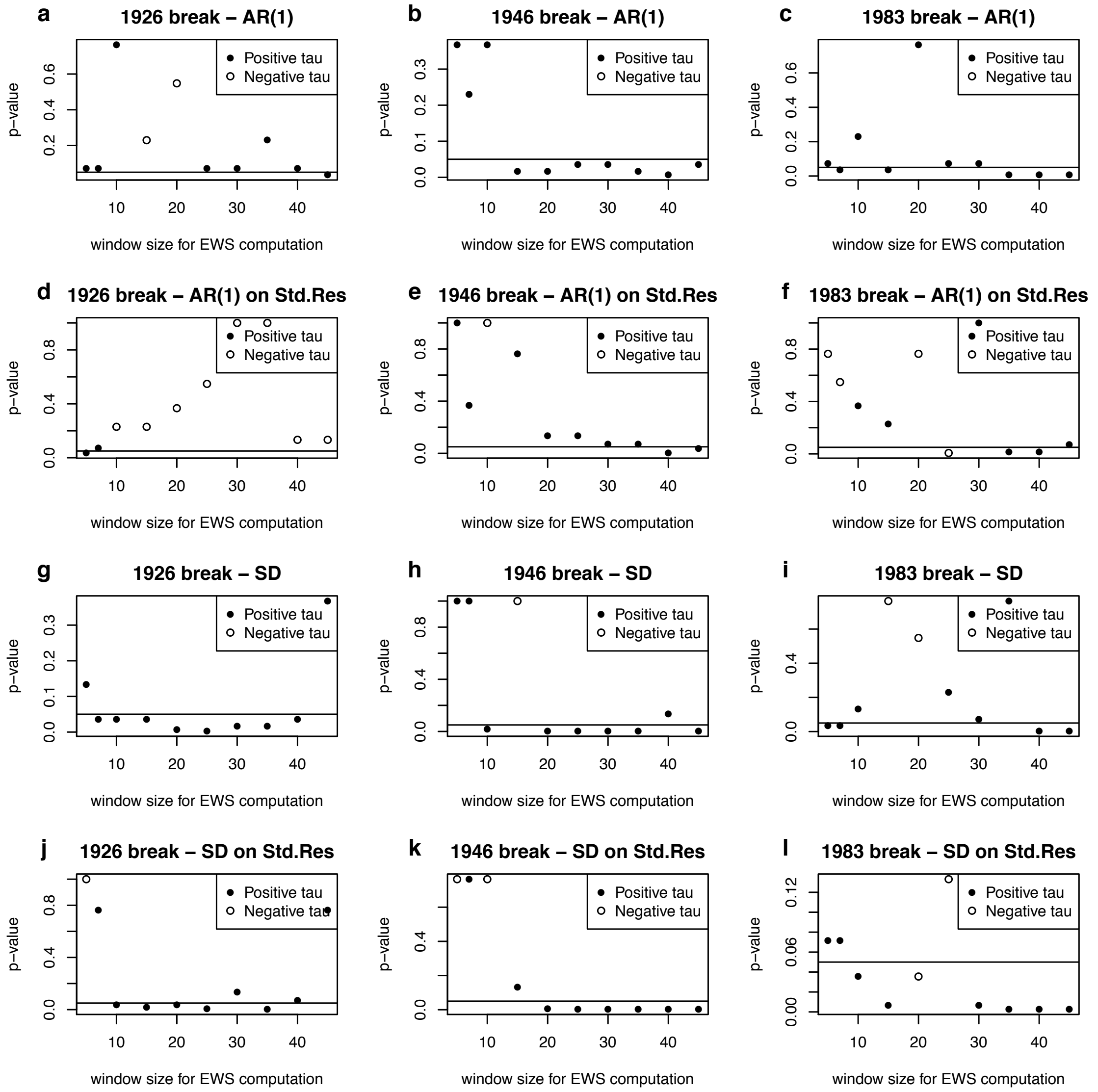


**Figure 3.4 |** Significance of EWS for 6 samples window.

Significance (*p*-value) and sign of the trend in (a, b, c, d, e, f) autocorrelation (AR(1), and (g, h, i, j, k, l) variance (SD) before each transition identified by Changepoints Analysis. Transitions are shown chronologically by column from left to right. The window used to obtain Mann-Kendall's tau (sign, positive or negative displayed by full and empty circles respectively) and *p*-value (significant level of 0.05 delimited by the horizontal line) is 6 samples. The trends in AR(1) and SD were calculated for raw DCA1 signals (a, b, c: AR(1); g, h, i: SD) and DCA1 residuals standardized for irregular spacing in time (see Methods in the main text) (d, e, f: AR(1); j, k, l: SD).

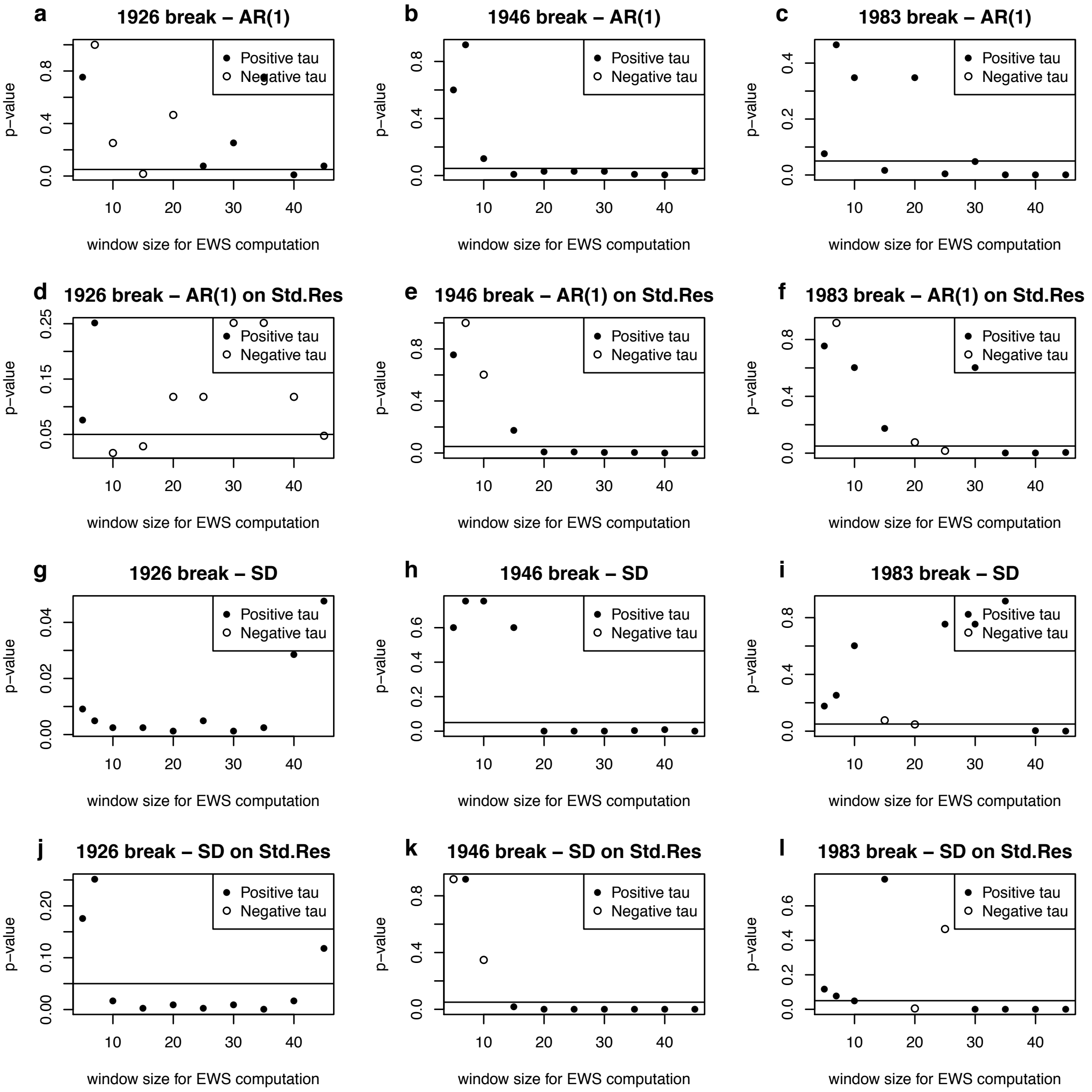


**Figure 3.5 |** Significance of EWS for 8 samples window.

Significance (*p*-value) and sign of the trend in (a, b, c, d, e, f) autocorrelation (AR(1), and (g, h, i, j, k, l) variance (SD) before each transition identified by Changepoints Analysis. Transitions are shown chronologically by column from left to right. The window used to obtain Mann-Kendall's tau (sign, positive or negative displayed by full and empty circles respectively) and *p*-value (significant level of 0.05 delimited by the horizontal line) is 8 samples. The trends in AR(1) and SD were calculated for raw DCA1 signals (a, b, c: AR(1); g, h, i: SD) and DCA1 residuals standardized for irregular spacing in time (see Methods in the main text) (d, e, f: AR(1); j, k, l: SD).

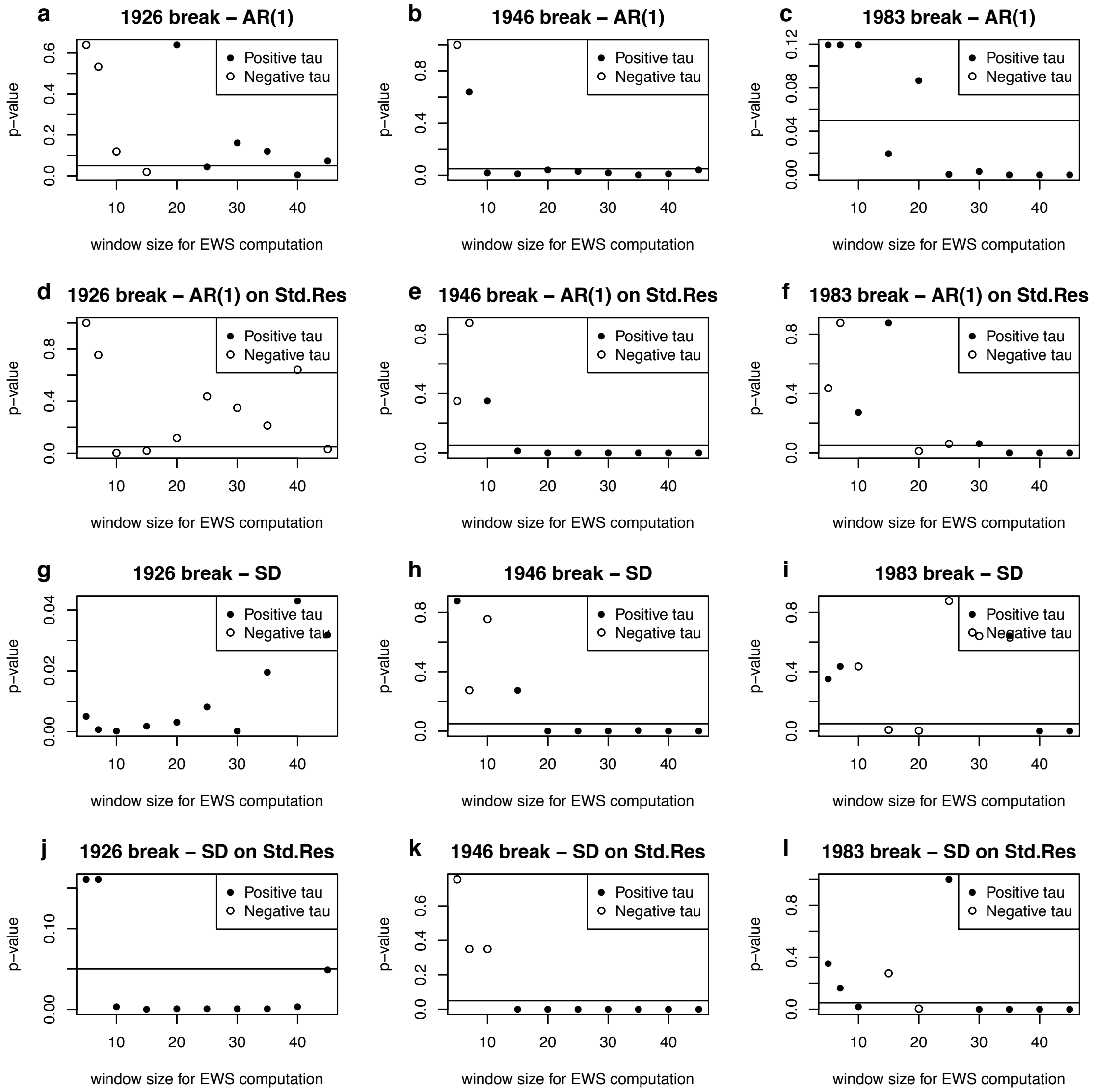


**Figure 3.6 I** Significance of EWS for 10 samples window.

Significance (*p*-value) and sign of the trend in (a, b, c, d, e, f) autocorrelation (AR(1), and (g, h, i, j, k, l) variance (SD) before each transition identified by Changepoints Analysis. Transitions are shown chronologically by column from left to right. The window used to obtain Mann-Kendall's tau (sign, positive or negative displayed by full and empty circles respectively) and *p*-value (significant level of 0.05 delimited by the horizontal line) is 10 samples. The trends in AR(1) and SD were calculated for raw DCA1 signals (a, b, c: AR(1); g, h, i: SD) and DCA1 residuals standardized for irregular spacing in time (see Methods in the main text) (d, e, f: AR(1); j, k, l: SD).

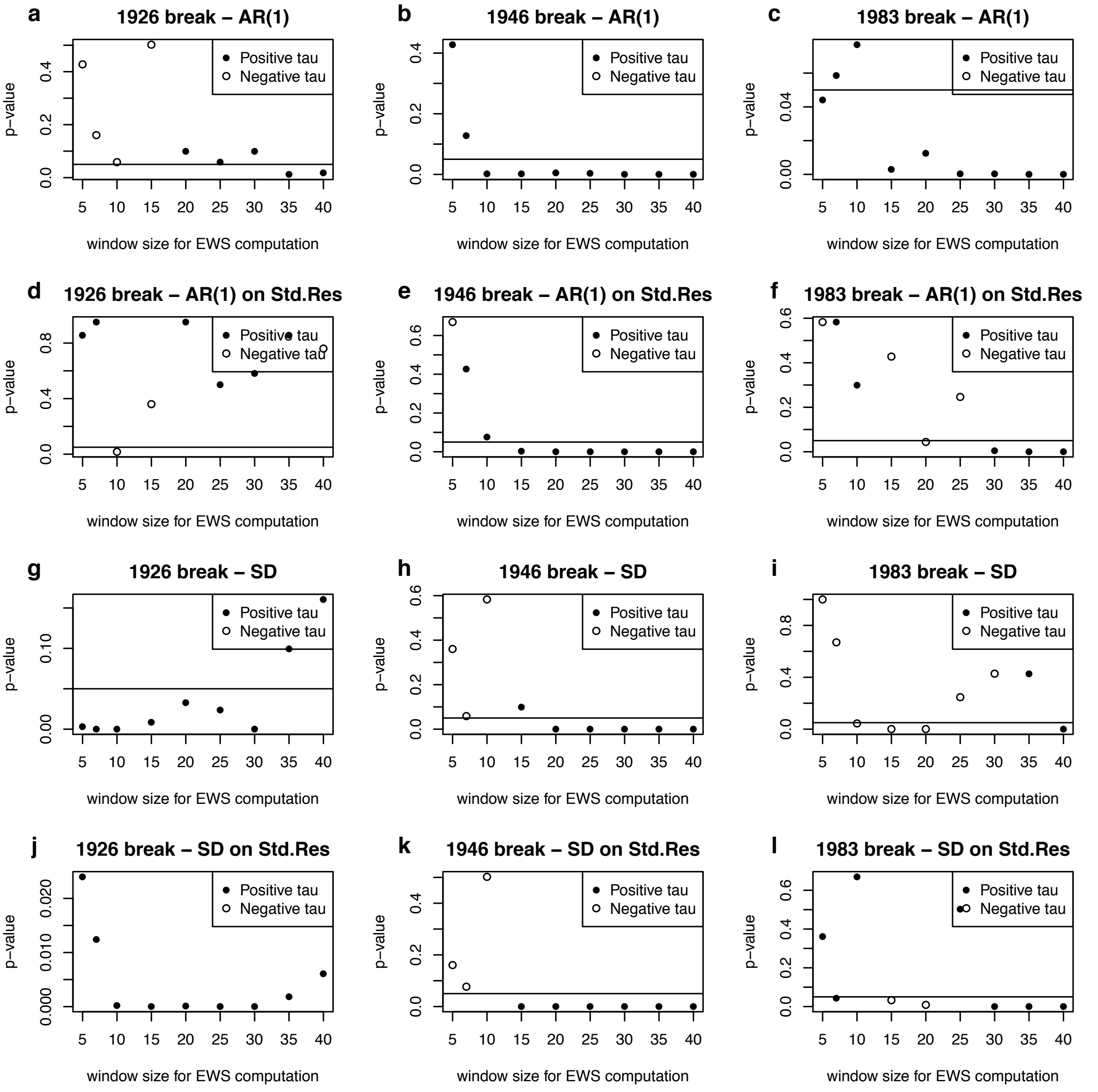


**Figure 3.7 I** Significance of EWS for 12 samples window.

Significance (*p*-value) and sign of the trend in (a, b, c, d, e, f) autocorrelation (AR(1), and (g, h, i, j, k, l) variance (SD) before each transition identified by Changepoints Analysis. Transitions are shown chronologically by column from left to right. The window used to obtain Mann-Kendall's tau (sign, positive or negative displayed by full and empty circles respectively) and *p*-value (significant level of 0.05 delimited by the horizontal line) is 12 samples. The trends in AR(1) and SD were calculated for raw DCA1 signals (a, b, c: AR(1); g, h, i: SD) and DCA1 residuals standardized for irregular spacing in time (see Methods in the main text) (d, e, f: AR(1); j, k, l: SD).

## 3.3 | INVESTIGATING POTENTIAL BI-STABILITY OF A DRIVER ON ECOSYSTEM RESPONSES

In Chapter 1 and earlier when introducing the method, I mentioned the main limitation of GAM i.e. the method is not designed to account for any potential bi-stability. In Chapter 5, we propose a method to test the existence of several regime of vulnerability. This section brings more details on the method; it is a Supplementary Materials to the manuscript of Lake Geneva (Bruel *et al.*, Under Review).

Our approach can be declined in three steps. First, the main dynamics i.e. transitions within the cladoceran assemblage (Figure 3.8) were assessed over time. Then, the environmental drivers of those transitions were identified, in order to disentangle those due to local human impacts from those attributed to climate variability. This step allowed defining time-periods of 'pristine' and 'anthropogenized' status of Lake Geneva. Finally, we quantified the amounts of climate-driven ecological changes between these two references time-periods, in order to test whether the lake ecological vulnerability to climate has changed over time.

### 3.3.1 | CHANGES THROUGH TIME

The main dynamics of the cladoceran community over time were summarized using Principal Component Analysis (PCA), after Hellinger transformation of the percent data, and significant changes in the mean of the PCA scores were detected using Changepoint analysis (Killick *et al.*, 2016). The significance of these change points was tested comparing the number of detected change points as compared to those that can be on average expected for a random series, using the Pruned Exact Linear Time (PELT) method constrained by a penalty. Low penalty value results in the detection of a high number of change points while increasing penalty value decreases the final number of change points detected. The penalty was determined by the incremented Akaike information criterion (AIC) method and verified manually by conducting an elbow plot.

The two first ordination axes accounted together for 90 % of the total variability in the dataset (Figure 3.9). The highest scores on the first component (PC1, 83 % of the projected inertia) (loadings > 0.9) were correlated with the percentage contribution of *Sida crystallina* var. *limnetica*, that occupies both the pelagic and littoral zone throughout its life, and the pelagic *Eubosmina longispina*. The pelagic *Daphnia* sp., and in a lesser extent the predator *Leptodora kindti* showed the lowest loadings on PC1. The second component (PC2, 7 % of the projected inertia) was positively correlated with *Sida crystallina* var. *limnetica*, and negatively with *Eubosmina coregoni, E. longispina*, and *Leptodora kindtii* (loadings < 0.2).

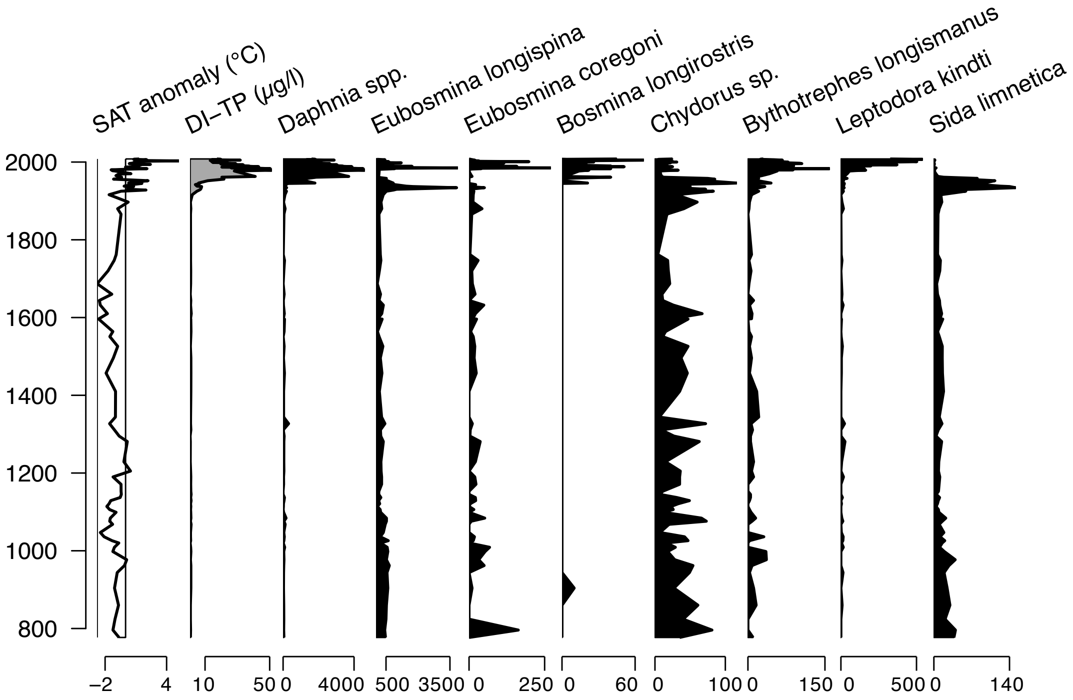


**Figure 3.8 l** Palaeostratigraphy of Lake Geneva cladoceran communities from 777 to 2008.

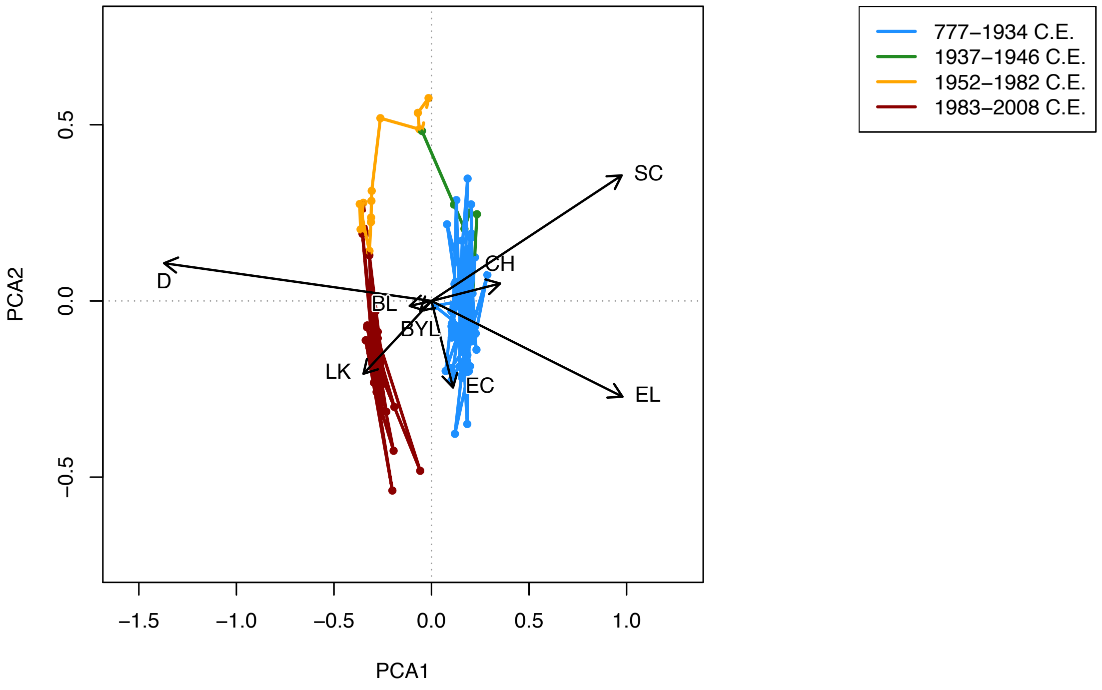


**Figure 3.9 l** Biplot of the first two principal components on cladoceran assemblage.

Species code: SC: Sida crystallina var. limnetica, CH: Chydorus sp., EL: Eubosmina longispina, EC: Eubosmina coregoni, BYL: Bythotrephes longismanus, LK: Leptodora kindtii, BL: Bosmina longirostris, D: Daphnia spp.

Changepoints analysis with a penalty chosen by the AIC resulted in the detection of one significant change point on PC1, in 1946 / 1952, and two on PC2, in 1934 / 1937 and 1981 / 1982. The same change point analysis was conducted on the bootstrapped series of PC1 and PC2 with 1000 iterations, showing an average of 0 change-point, indicating that the number of transitions detected was not the result of chance but, instead, of a specific ordination in time.

### 3.3.2 I IDENTIFICATION OF MAJOR FORCINGS

The relative contribution of changes in I-TP (Chapter 2) and climate (summer air temperature (SAT) anomalies, Büntgen *et al.*, 2006) to the dynamics of PCA scores were assessed by using the Generalized Additive Models (GAMs, Wood, 2016). The final GAMs were chosen by computing models using I-TP and SAT as covariates, and the best models were chosen following the Akaike Information criteria. Then, the choice to include or not a correlation structure (AR(1) or CAR(1) to account for uneven sampling) was conducted using the log-likelihood of each model . The competing forcing variables and their effects were separated based on the computed contribution each covariate made to the fitted model (Simpson & Anderson, 2009).

The final GAM for PC1 included a significant smooth term for I-TP (F= 148.2, p < 0.001). A correlation structure for the model errors was not supported by a likelihood ratio test (log-likelihood of 139.39 vs. 111.98 for a model with a correlation structure), and the two models provided indeed the same fit for the observed data. Therefore, the simplest model (without the correlation structure) was retained. The fitted smooth functions for the covariate is shown in Figure 3.10a, and the fit between predicted values and observations is presented on Figure 3.10b ($R^2$= 0.92). The fitted relationship between PC1 scores and SAT anomaly was nonlinear and used 6.52 of effective degree of freedom (EDF). I-TP contributed strongly to the shift of PC1 scores from positive to negative values at ca 10 µgP.$l^{-1.}$ Above 20 µgP.$l^{-1}$, I-TP contributed in maintaining low PC1 scores but the relationship was less steep. Thereby, the pelagic *Eubosmina longispina* and the macrophyte associated *Sida crystallina* var. *limnetica* dominated at low I-TP, while *Daphnia* spp. relative abundance increased along with I-TP, up to 20 µgP.$l^{-1.}$ at which its supremacy is stable and established.

Consistently, I-TP contribution to the time-series of PC1 scores switched in the mid-1950s, confirming that eutrophication drove the major ecological alteration of Lake Geneva ecological status over the last 1400 years (Figure 3.11). The lag between the first detected changes in 1946 / 1952 and the important shift in 1961 / 1963 marks a transition period during which the food elemental quality improved, benefiting to *Daphnia* spp. that has high stoichiometric requirements (Urabe, Clasen & Sterner, 1997; Elser, Hayakawa & Urabe, 2001; Hessen, Færøvig & Andersen, 2002), but under a threshold that prevented any restructuration in the phytoplankton assemblage (Chapter 2, DeMott & Gulati, 1999). Furthermore, the maintenance of *S. crystallina* followed by its decline hint that no changes in algal biomass took place in the 10-20 µgTP.L$^{-1}$ range, since the resulting light limitation would have compromised the maintenance of the macrophyte-associated specie. Beyond 20 µgTP.L$^{-1}$, *Daphnia* spp. made the most of the nutrient driven changes in the phytoplankton community structure while the herbivorous *E. longispina* suffer from their lower feeding efficiency compared to the larger phytoplankters. Besides, the habitat-demanding *S. crystallina*, that had been present continuously since 563, almost vanished from Lake Geneva from 1963. Such a pattern has been consistently observed in all the deep peri-alpine lakes in which phosphorus concentrations increased in the mid-20th (Manca *et al.*, 2007; Alric *et al.*, 2013).

This major reorganization in the cladoceran communities due to anthropogenic eutrophication was set as the limit between a 'pristine status' and an 'anthropogenized status' of the lake. Besides, it matched perfectly the most reasonable limit set up for the beginning of the Anthropocene (Zalasiewicz *et al.*, 2017). Because it was asserted that PC1 gathered all the eutrophication driven changes in the cladoceran assemblages, other PCs accounted for ecological changes attributed to other environmental constrains, climate being one of the candidate.

When GAM was applied on the 1400 years of PC2 scores, none of the factors was detected as a significant driver of the millennial variability (all combination tested), confirming

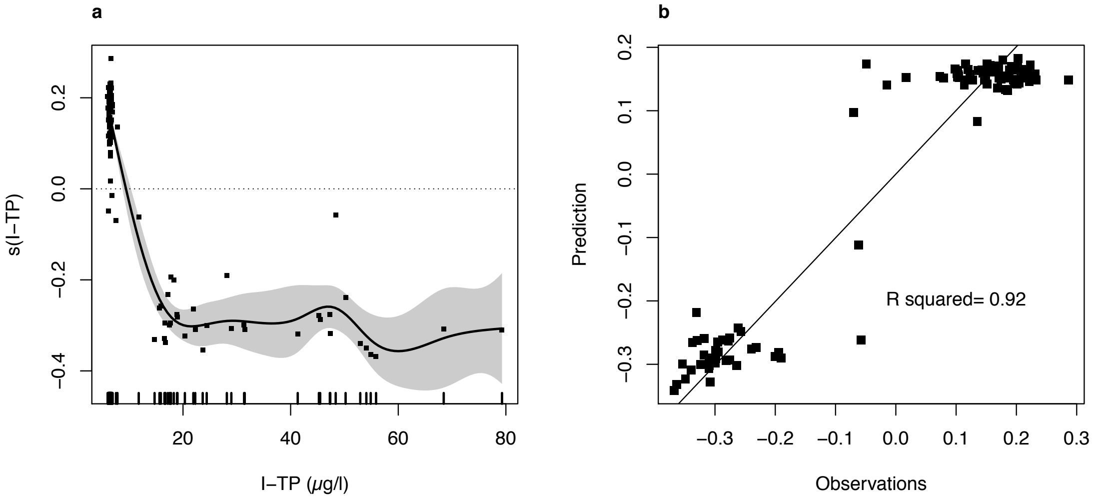


**Figure 3.10 I** Fitted smooth function and predicted vs. observed values using I-TP as covariate to explain PC1 variability.

(a) The fitted smooth functions for I-TP from the final GAMs for the PC1 scores for Lake Geneva cladoceran assemblage. The thick marks inside the panel on the x-axis show the distribution of observed values for the covariate. (b) Predicted vs. observed PC1 scores.

that PC2 variability summarized ecological changes that were independent from changes nutrient concentrations. At this time-scale, climate variability was neither identified as a significant covariate, while a previous palaeo-study based on the past 150 years (i.e. the anthropogenized time-period) had found a significant impact of recent climate warming in the prediction of cladoceran assemblage (Alric *et al.*, 2013). The fact that the structuring role of climate variability did not extend back to the last millennium was a first reason to suspect change in regime of vulnerability to climate.

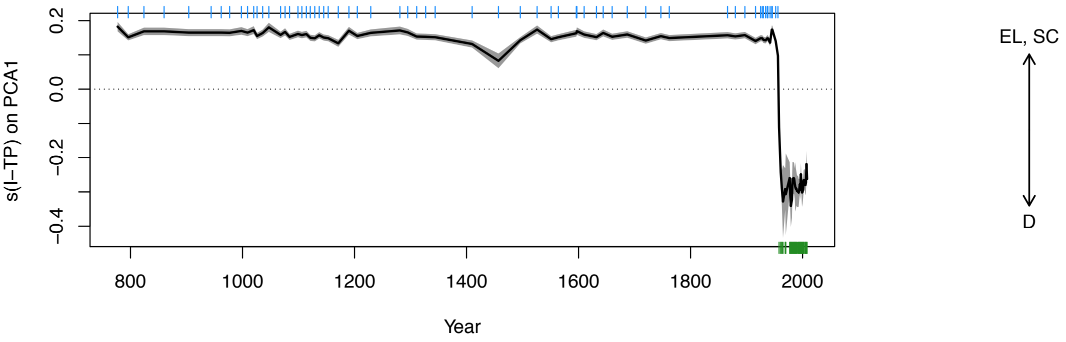


**Figure 3.11 I** The contribution of I-TP to PC1.

Right panel: species favoured when contribution is significant. Years with significant contributions are identified by coloured tick on top and bottom axes. EL: *Eubosmina longispina*, SC: *Sida crystallina* var. *limnetica*, D: *Daphnia* spp..

### 3.3.3 | RESPONSES TO CLIMATE VARIABILITY BEFORE AND AFTER LOCAL HUMAN IMPACTS

GAM was thereafter applied separately on PC2 scores for the two time-periods (‘pristine’ 773-1946, 1952-2010 ‘anthropogenized’). Each dataset contained 63 and 38 datapoints respectively. A sensitivity analysis was besides conducted in order to evaluate how much our conclusions depended on the date considered as the limit between the pristine status and an anthropogenized system. In that aim, the analysis was repeated for all possible dates ranging from 1114 to 1987 (Figure 3.12). This way, 20 points at least were left for fitting a model in every group. We then performed GAM with SAT anomalies as the main covariate for the different subset. For each run, a correlation structure for the model errors was not supported by a likelihood ratio test.

The two forcings variables (I-TP and SAT anomaly) could only explain a really low amount of the total deviance in PC2. Yet, the deviance explained increases dramatically when the hypothesis of two regimes of vulnerability of the cladoceran communities to climate variability is tested.

Indeed, climate variability was not identified as a significant driver of PC2 scores during the pristine state (F= 3.445, p-value= 0.07, Dev. Expl.= 4.9%, Fig. Figure 3.13c) while its contribution was significant for the anthropogenized time-periods (F= 7.108, p-value= 4.79 $10^{-4}$, Dev. Expl.= 44.8%, Figure 3.13d). Consistently with previous results by Alric *et al.* (2013) the fitted values adequately reproduced the observed scores, and the model was satisfactory. Increasing SAT contributed to push PC2 scores towards negative values, i.e. the slope of the relationship tying the constraint to the response was negative. Pushing the limit date backward down to the early 18th century led to the same conclusions (e.g. Figure 3.13f). Pushing the limit forward (>1956) concluded to a weak relationship between climate variability and ecological response in the so-called 'Pristine state' with yet a positive slope (e.g. Figure 3.13a). Yet, the models ability to predict observed scores was actually poor for a limit sate set >1956 and in all cases the slope tying SAT to scores was always positive. Thereby, even if the ecological status of the lake might have been responding to climate variability in the so-called pristine state, climate-driven responses (changes in cladoceran assemblages) would have been radically different to those currently observed.

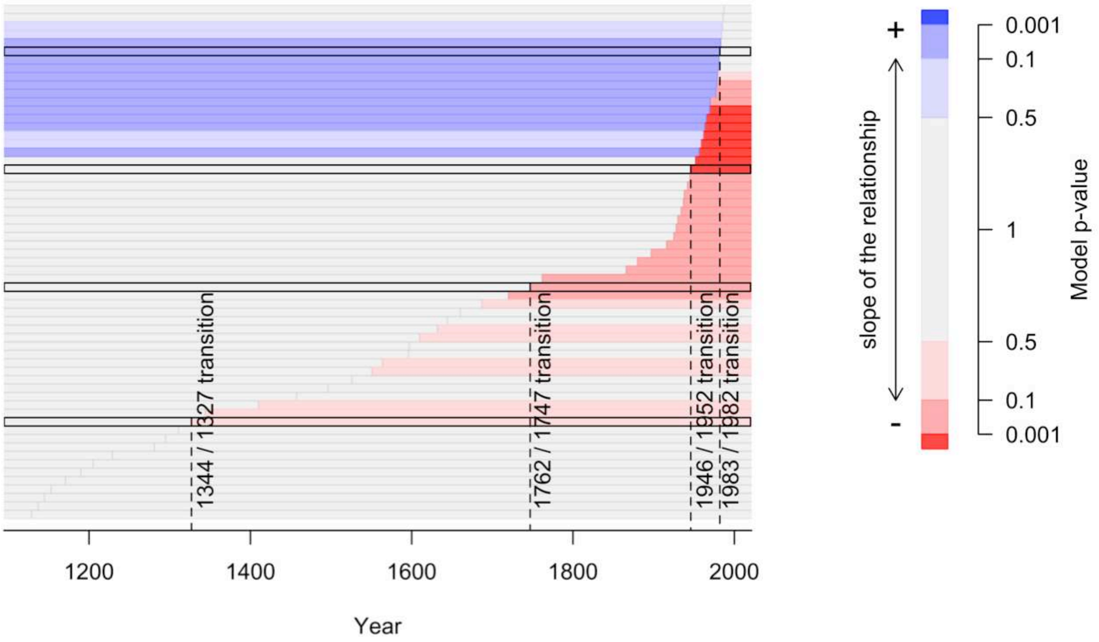


**Figure 3.12 l** Test of windows significance for lake ecological vulnerability to climate variability.

The x-axis set the limit date at which the datasets were split. The different colours reflect the significance of the model fitted to SAT anomalies as well as the slope of the relationship in order to depict the change in the regime of vulnerability for the time period before and after the limit date. Results for the four examples indicated by dotted lines are provided in details in Figure 3.13.

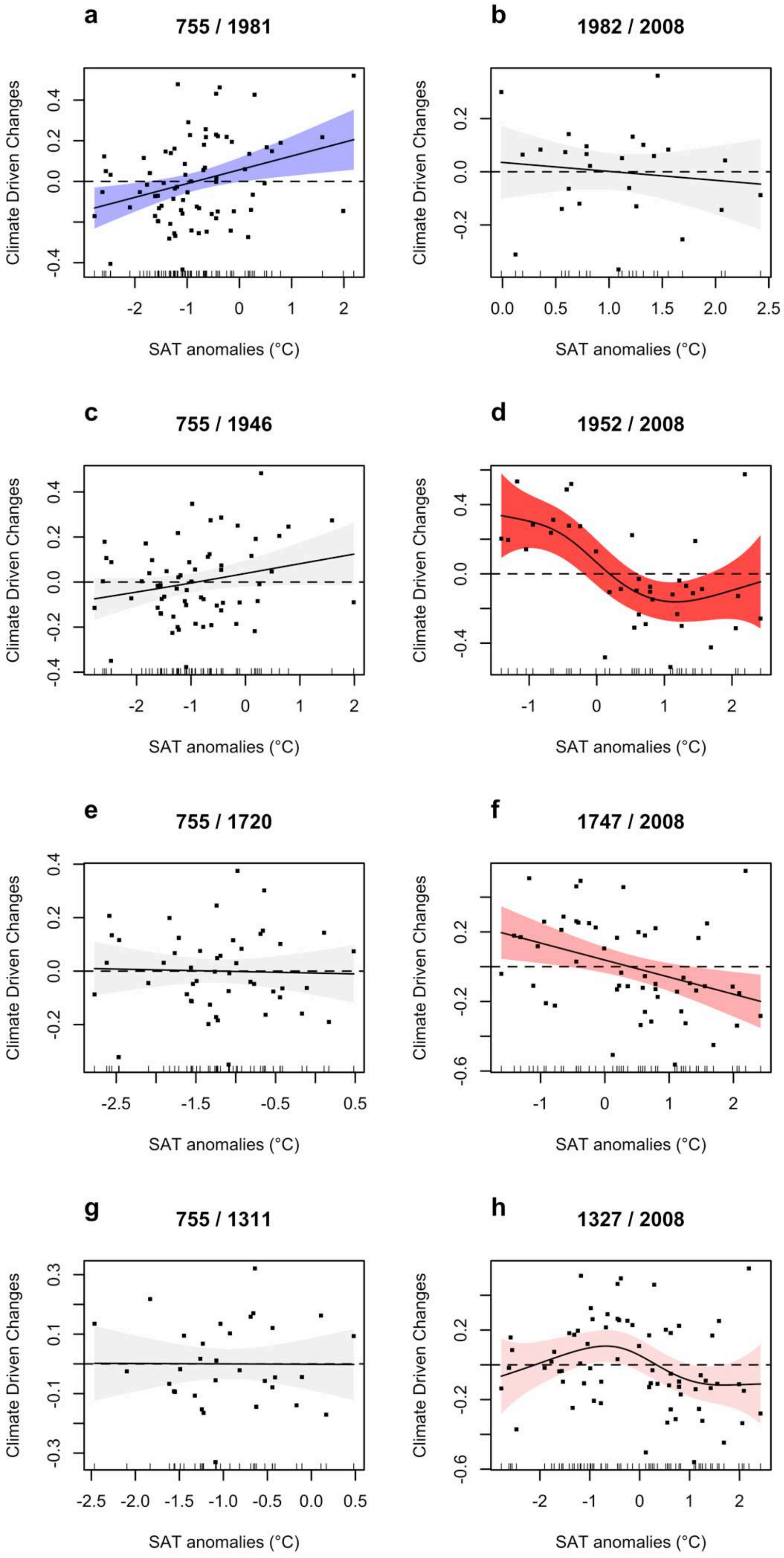


**Figure 3.13 I** Fitted smooth functions for SAT anomalies for different periods.

## 3.4 | COMPARISON OF CLADOCERAN TRAJECTORIES ACROSS SYSTEMS

Our last question required quantifying the different levels of vulnerability to climate variability across systems.

Species abundance according to time was obtained for each lakes of the study resorting to palaeo-ecological approach. However, we needed a standard approach to identify the main trends in the assemblage. We hypothesized that changes in the assemblage were driven by change in the environmental conditions (principally eutrophication and climate change, two important threats to freshwater bodies). No methods could be found in the literature to compare ecological responses to climate warming across systems. We explored several directions and present here some methods that we thought to be relevant, and some that we later rejected. We chose to also present the methods that we finally discarded because the choice greatly impacted our analysis. A comparison of the performances of different methods on several datasets can be useful to other investigators.

The first objective was to describe the trajectory of the different lakes together. We assessed whether we could detect a trajectory that was common between lakes. We used multiple factor analysis (MFA) implemented in the *ade4* package (Dray, Dufour & Chessel, 2007). MFA is an extension of principal component analysis (PCA), tailored to handle multiple data tables, that measures sets of variables collected on the same observations (Abdi, Williams & Valentin, 2013). To do so, we first delimited three periods for each lake: a pristine period, before any modification on the assemblage could be observed, a eutrophication period, during the maximum eutrophication (usually the second half of the 20th century), and the recent period (2000-2010). The delimitation of these periods (as seen on Figure 3.14) was done based on reconstructed TP levels or from monitoring data, and only when we could qualify with confidence that the level of phosphorus was low/high. Lake Como and Lake Maggiore were ruled out from the MFA computation, as their short-time coverage does not guarantee the observation of the pre-eutrophication ('pristine') period. We then randomly sampled three samples among each of these three subsets to create a new matrix. We obtained 11 matrices (one for each lake except Lake Como and Lake Maggiore – two sites in Lake Garda) of n species over 9 samples (3 sub-samples for each of the 3 periods). These matrices were merged together to form the matrix used for MFA. MFA then proceeds in two steps: First it computes a PCA of each data table and 'normalizes' each data table by dividing all its elements by the first singular value obtained from its PCA. The first singular value is the square root of the eigenvalue of the first dimension, which can be seen as a variance. In other words, this step is no more than a Z-score normalization (Abdi *et al.*, 2013). Second, all the normalized data tables are aggregated into a grand data table that is analysed via a (non-normalized) PCA that gives a set of factor scores for the observations and loadings for the variables (Abdi *et al.*, 2013). In addition, MFA provides for each data table a set of partial factor scores for the observations that reflects the specific 'view-point' of this data table. We resampled 30 times from the initial matrix and repeated the following steps to strengthen the results. Figure 3.15 illustrates the different steps.

The objective of the MFA was two-fold. First, we wanted to check whether or not we could accurately discriminate different periods from their species assemblage, and consequently identify major ecological gradients. Secondly, providing the first objective was successful, we retrieved the species coordinates for the selected ecological gradient. The aim was to evaluate whether or not the same species were always responsible for driving the relationships. Indeed, MFA does not recognize similar species among lakes (they were all coded with 'namelake_specie' during the computation), as its objective is to discriminate the different sites from the set of different observations. As a consequence, we used some data mining approach to check the frequency of contribution of each species in explaining the variability.

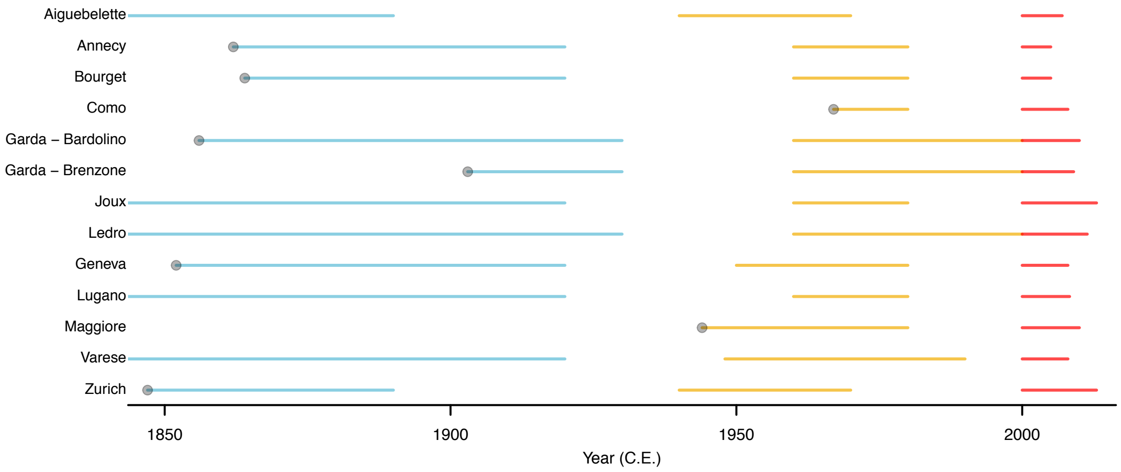
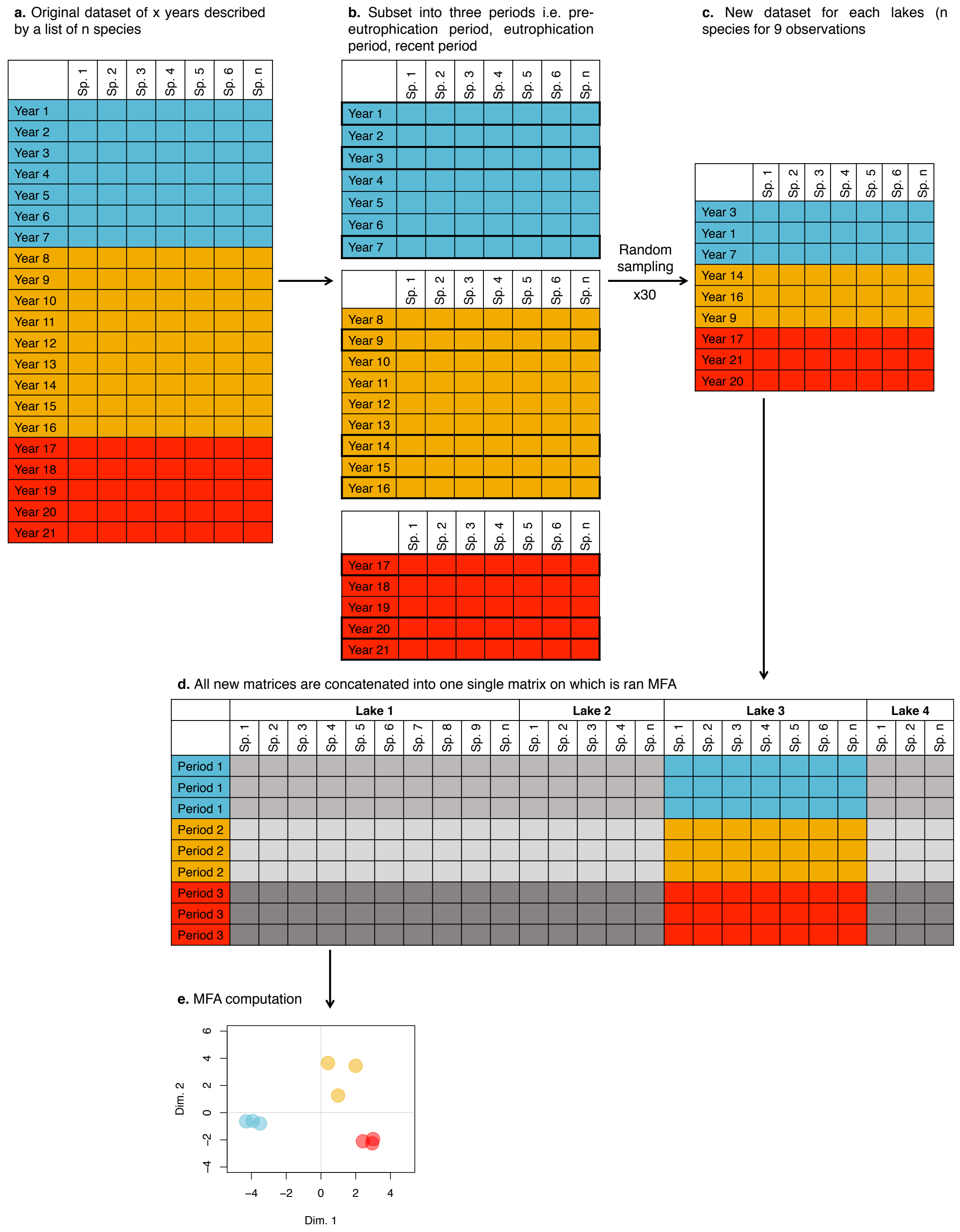


**Figure 3.14 I** Delimitations of periods for MFA computation i.e. pre-eutrophication period (blue), maximum period of eutrophication (orange) and recent period (red).
Black dots indicate the beginning for each palaeo-sequence (if there is no grey dot, then the record started before 1850). Lakes Como and Maggiore had sequences too short to cover the pre-eutrophication period.



**a.** Original dataset of x years described by a list of n species

**b.** Subset into three periods i.e. pre-eutrophication period, eutrophication period, recent period

**c.** New dataset for each lakes (n species for 9 observations

**d.** All new matrices are concatenated into one single matrix on which is ran MFA

**e.** MFA computation

**Figure 3.15 I** Steps of the MFA computation.

(a) For each original matrix of n species observed for x years for each lake, three periods were identified: a pre-eutrophication period (blue), a eutrophication period (orange), the recent period (red). (b) The original matrix was subsequently divided in three submatrices. (c) Three date samples were taken from each of these submatrices and merged together into a new matrix. This process was repeated for each lake, in order to to build a large dataset (d) that gathered an average of 157 observations for 9 individuals (i.e. periods) divided into 11 groups (the lakes). (e) MFA was computed from this final matrix. Steps (c) to (e) were repeated 30 times to generate replicates.

#### 3.4.1.1 | Results

Over the twentieth century, freshwater bodies have been undergoing tremendous stress due to local human impact (Smith, 2003; Jenny *et al.*, 2016). TP abatement did not guarantee the recovery of systems as some are still displaying lower functioning (Moreno-Mateos *et al.*, 2017), or alternatively stayed in a degraded state. Confounding effects of climate change are also believed to add a supplementary burden in the restoration process (Battarbee *et al.*, 2005; Moss *et al.*, 2011). Three scenarios of eutrophication were observed in the sample of lakes we got to study herein. Lake Zürich displays an original eutrophication trajectory as it was the first one to turn eutrophic as soon as the late 19th century. A second wave of eutrophication took place in the second part of the 20th century, following the end of World War II. The lake is now on a restoration trajectory. The second scenario of eutrophication applies to almost all the lakes of the peri-alpine region (Lakes Aiguebelette, Annecy, Bourget, Geneva, Joux, Lugano, Maggiore, Varese). Theses lakes underwent initial changes in their nutrient levels as soon as the 1920s-1930s. This slight and early departure from the original trophic state was revealed by a common increased abundance of *Daphnia* spp. subfossil remains, a validated indicator of early eutrophication stages (Alric *et al.*, 2013; Bruel *et al.*, 2018). The following part of the story for each lake depended on the presence or absence of early management decisions but also some factors directly linked to the land use and population density on the watershed. When no action was undertaken, lakes shifted to a eutrophic state. For instance, local managers were prompt to react in Lake Annecy, and the lake concentrations remained relatively low. On the other hand, restoration efforts were important but came late in Lake Bourget and Lake Varese that displayed higher maximum level of TP. However, from the late 1970s and until the 1990s, all lakes managers adopted management practices that could restore lakes water quality. The extent of maximum P level varies greatly among systems (Varese > Lugano > Bourget > Geneva > Joux > Aiguebelette > Annecy). The present P mirrors this distance between the oligotrophic and eutrophic state, as Lakes Varese is still eutrophic in the 2010s. Finally, the last scenario of eutrophication applies to Lakes Ledro and Garda. These two lakes located at the Eastern part of our study site are still not on a stable restoration trajectory, as mirrored by DI-TP (Milan *et al.*, 2017). As a result, the effects of eutrophication may override the effects of climate warming, or, under our assumption detailed in the previous chapter further increase their vulnerability to climate change.

The good discrimination of the different periods allows identifying the major ecological gradients (Figure 3.16). This means that specific assemblages contained enough information for the MFA to discriminate the different periods.

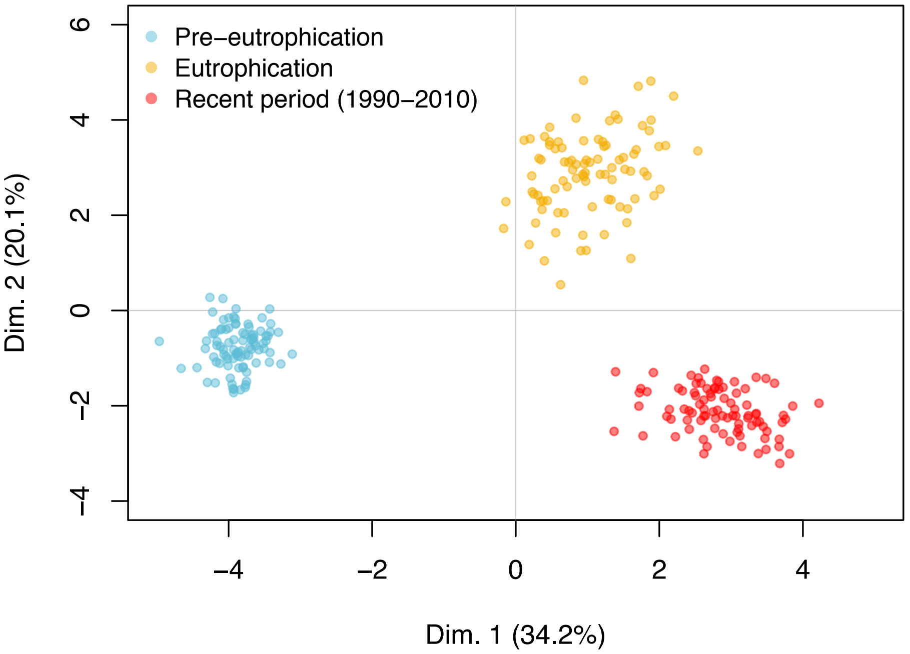


**Figure 3.16 l** First factorial plan of the individual scores for the MFA computations (30 replicates). The colours refer to the different periods i.e. 'Pre-eutrophication' or 'Pristine' (blue dots, before any modification on the assemblage), 'Eutrophication' (orange dots, period for which the maximum TP values were recorded for each lakes), 'Recent period' (red dots, the 2000-2010 period).

We then considered the species that contributed the most to each axis, i.e. those which loadings <-0.3 or >0.3 for each MFA. (Figure 3.17). The maximum variability across the study lakes (Axis 1, 34%) is clearly driven by modifications in the pelagic assemblage (Figure 3.17 a), consistently with the pelagic location at which cores were retrieved. Besides, the same species alternatively contributed in driving changes in the pre-eutrophication assemblage (negative score on Axis 1, Figure 3.16) and the recent assemblage (positive score on Axis 1, Figure 3.16). This indicates that the dominance of species can be peculiar to systems, or at least system types (e.g. Lakes Annecy, Bourget, Geneva recent assemblage are all characterised by the return of *Eubosmina longispina*). Axis 2, on the other hand, most likely reflects the eutrophication gradient, i.e. are characterized by assemblages characterizing the different maximum eutrophication degrees lakes reached over the last century. Fundamentally new assemblages characterized lakes that were the most impacted by eutrophication (MFA, similarly to PCA, maximize the variance in each dimension, see principle Figure 3.1). Core samples from the 'eutrophication period' show positive scores on Axis 2 (Figure 3.16). The pelagic grazers *E. longispina* and *Daphnia* spp., as well as the predator *Leptodora kindti*, were most likely to be found during these periods (positive loadings). Some littoral taxa were also observed, notably two large littoral species, *Alona quadrangularis* and *Acroperus harpae* (Figure 3.17). The first one is ubiquitous and lives in both sediment and macrophytes, mostly in eutrophic lakes (Bjerring *et al.*, 2009). *A. harpae* on the other hand is a species associated to macrophytes only and lives in oligotrophic waters. Its disappearance from Lake Lugano was used as a marker of eutrophication (Ravera & Parise, 1978), but it remained present during the eutrophication period in Lake Joux and Lake Zurich. In Lake Garda (Brenzone station), the species abundance has been decreasing since the 1970s and has been absent in the most recent period (since the 1990s). However, the most interesting feature may be the homogenization of the communities for systems driving the relation towards positive scores on Axis 2 (Vonlanthen *et al.*, 2012; Taranu *et al.*, 2015; Monchamp *et al.*, 2017). The significant correlation (Spearman rank correlation, rho= 0.67, p= 0.024) between lakes contributing to Axis 2 (Dev. Expl.= 20%) and their maximum level of eutrophication (Figure 3.18) support the fact that this dimension represents the eutrophication gradient.

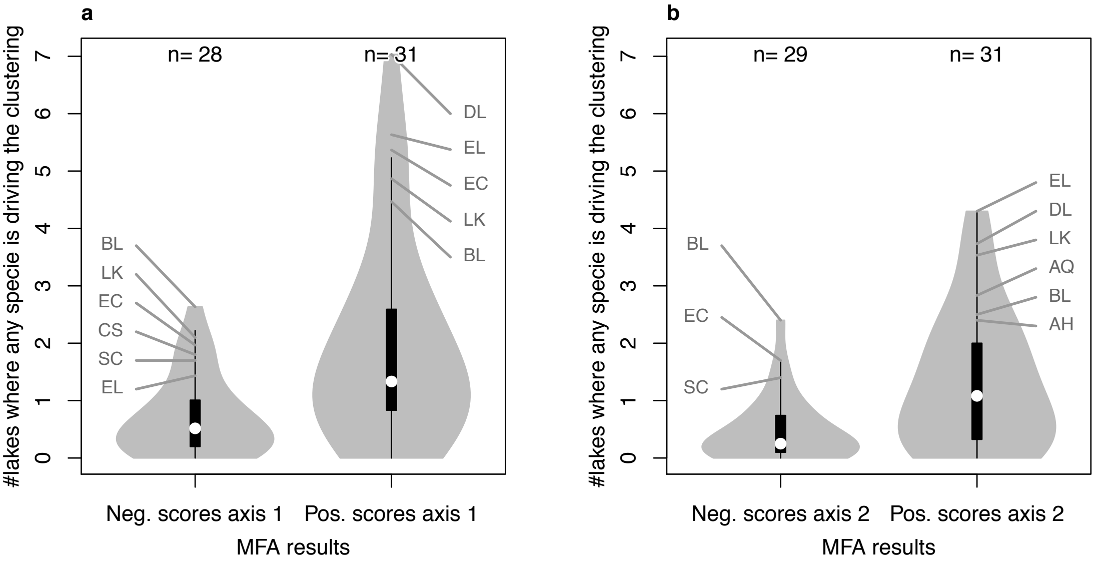


**Figure 3.17 I** Violin plots showing the probability density, median (white dot) and interquartile range of the number of lakes for which any of the n species (stated above each violin plot) contributed in driving the assemblage.

Plotted for (a) axis 1 and (b) axis 2 of the MFA. For each replicate MFA (30 replicates), we kept the species that contributed to the constructions of the axis. We only selected the species with coordinates >0.3 or <-0.3. Then, we counted the occurrence of each species in each axis, and divided the score by the number of replicates (i.e. 30). This shows that the years with positive eigenvectors on axis 1 and 2 are more likely to be characterised by the same species than the years with negative eigenvectors on the selected axis. The species with the highest coordinates are indicated with their code. AH= *Acroperus harpae*, AQ= *Alona quadrangularis*, BL= *Bosmina longirostris*, CS= *Chydorus sphaericus*, DL= *Daphnia* spp., EC= *Eubosmina coregoni*, EL= *Eubosmina longispina*, LK= *Leptodora kindti*, SC= *Sida crystallina.*

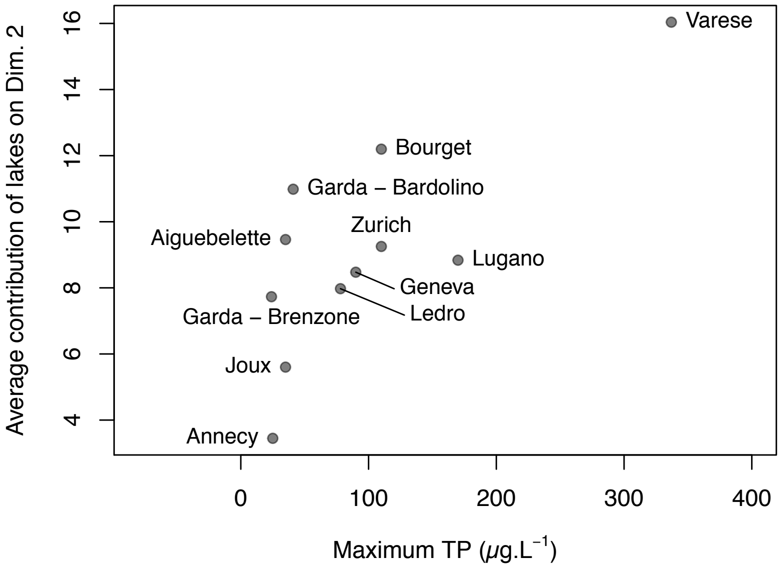


**Figure 3.18 I** Average contribution of lakes on the second dimension of the MFA versus the maximum TP ($\mu$g.L$^{-1}$) for each lake.

The correlation between the two vectors is significant (cor= 0.73, p= 0.011).

On the other hand, the first dimension (Dev. Expl.= 34%) shows either an effect or time, or an effect of climate warming. Because climate warming, displayed a monotonic trend over the past century, we cannot assess this from this analysis. However, with a high contribution on this first dimension are systems that contribute the most to the overall variability i.e. systems that are not following a linear pathway of restoration.

Lake Varese, Garda (Bardolino basin) and Ledro are the lower contributors to this dimension. These two lakes and sub-basin (Lake Garda – Bardolino) are systems that were either still eutrophic or undergoing eutrophication until the 2000s. Indeed, the maximum DI-TP concentration in the Bardolino basin is 41 µg TP.L$^{-1}$ in 2008 versus 25 µg TP.L$^{-1}$ in the Brenzone, deepest basin, and those values were reached during the 2000s. DI-TP shows significant offsets from monitoring TP (+10 µgP.L$^{-1}$ in Brenzone, +20 µgP.L$^{-1}$ in Bardolino, Figure 2.24), but trends are similar i.e. lower TP concentrations from the 2010s (Milan *et al.*, 2017).

To conclude on MFA, the analysis was efficient in showing the common eutrophication trajectory of the different lakes. In other words, eutrophication is a local driver with generalised impacts.

## 3.5 | ORGANIZATION LEVEL

### 3.5.1 | METHODS

We quantified the vulnerability at two levels: the community level, using principal curves (PrC) and principal component analysis (PCA) to sum up the general dynamics, and the specie level.

PrC (De'ath, 1999; Simpson & Birks, 2012) are a non- or semi- parametric alternative to PCA and correspondence analysis (CA). It sums up the information in one axis. PrC were computed for each lakes following Bennion *et al.* (2015b; 2015a) and using the *analogue* package (Simpson, 2007; Simpson & Oksanen, 2016). We follow Simpson & Birks (2012) and allow the spline degrees of freedom to vary between species. PCA axis 1 was used as the starting curve in the principal curve fit for all sites except Lakes Joux and Lugano where a CA axis 1 was used. These changes were needed to achieve a satisfactory fit with simple species response curves along the fitted PrC. However, PrC performs badly when different gradients are present, which is what we expect i.e. a response to a gradient of eutrophication and a response to a gradient of climate warming.

Multivariate ordination methods, on the other hand, are powerful tool to summarize the variability in an assemblage along several gradients into univariate data (i.e. principal components). As a consequence, in most cases, it is relevant to select more than one axis to fully apprehend the ecosystems gradients (Bruel *et al.*, Under Review, Chapter 5, 2018, Chapter 4; Bennion *et al.*, 2015b). Several ordination methods exist. Among them are detrended component analysis (DCA) and PCA, respectively used in Chapter 4 and Chapters 5-6. In here, we chose to use only PCA, but both would lead to the same information eventually. In fact, due to the way they are built, first and second components may put the emphasis on a different cluster of sites (in the case of palaeolimnology, a period of time), but eventually will carry the same information if a sufficient number of axes are selected. We illustrate this assertion with the data from Lake Varese (Chapter 4). DCA and PCA run on the same dataset of Lake Varese put respectively the maximum variability on the recent assemblage driven by climate change or on 1950-1980 period assemblage, corresponding to the eutrophication period (Figure 3.19). Conversely, the second axis either illustrates the warming gradient (PCA2) or the eutrophication phase (DCA2). In Chapter 4, we had selected DCA because it summed up the more variability (i.e. 46%). Figure 3.19 shows that, had we selected PCA, we would have identified all the changes linked to eutrophication on the first component (with the loss of the littoral diversity in the mid-1940s), and the changes linked to climate on the second components.

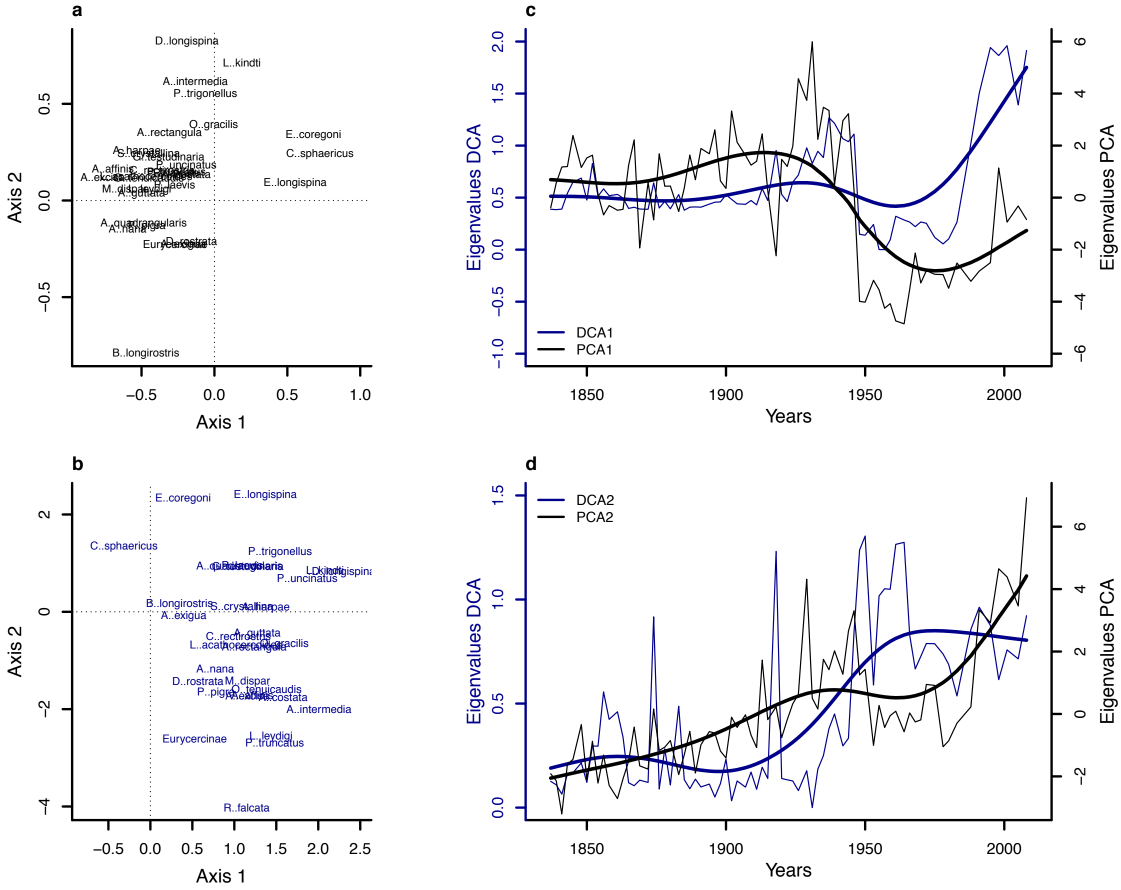


**Figure 3.19 I** Comparison of DCA and PCA classifications.

(a) Contribution of species to the Principal Component Analysis (PCA) first factorial plan. (b) Eigenvectors of species to the Detrended Correspondance Analysis (DCA) first two dimensions. PCA (blue lines) and DCA (black lines) ordination comparison on first (c) and second (d) dimension. On (c) and (d), the thin lines are the raw eigenvalues. Principal Curves were also fitted using the package *princurve* (Hastie & Weingessel, 2016) on individuals components to make the trends more apparent (thick lines).

While the eutrophication gradient was preserved for both Lakes Varese (Chapter 4) and Geneva (Chapter 5) on axis 1, and climate warming could be explained by axis 2, this may not be the case for each lake. Therefore, we carried out the analysis on the two first components for each lake and later selected the one which climate explained more vulnerability. PCA were fitted using the package *vegan* (Oksanen *et al.*, 2016).

### 3.5.2 | ADJUSTING FOR IRREGULAR SAMPLING

The density of observations varied strongly among and between cores. To make up for it, we interpolated linearly from point to point the raw data. This step did not aspect the overall ordination, as evidenced on Figure 3.20. The grey and coloured lines show the PC scores of the first factorial plan for respectively the raw and interpolated data. The lag between the scores is later lost as GAM normalised the scores in a preliminary step.

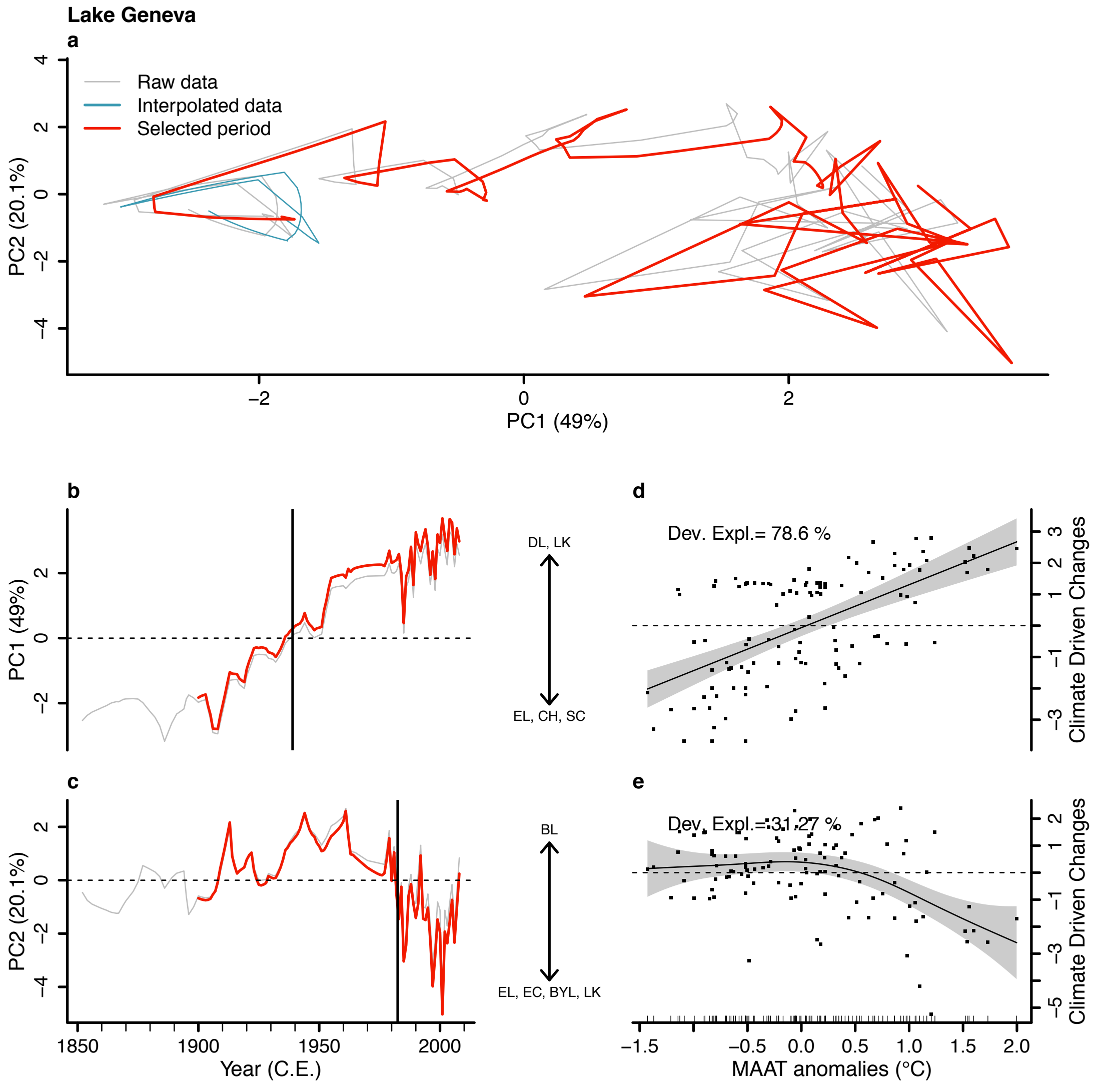


**Figure 3.20 |** Verification of PCA ordination with and without interpolation of the raw data.

(a) PCA run on raw data (grey) and interpolated data (color). (b) PC1 and (c) PC2 scores vs. time. Vertical bars shows main change-points identified with the changepoint method (see Chapter 4). Arrows on the right show species with high loadings on PC1 and PC2 respectively, codes are: BL= *Bosmina longirostris*, BYL= *Bythotrephes longismanus*, CH= *Chydorus* sp., DL= *Daphnia* spp., EC= *Eubosmina coregoni*, EL= *Eubosmina longispina*, LK= *Leptodora kindtii*, SC= *Sida crystalina*. (d) and (e) shows GAM result for both PC1 and PC2 using MAAT as a covariate.

When we later performed additive models, we used a continuous time first-order autoregressive (CAR(1)) process for the residuals, to account for the lack of independence between the observations (Simpson & Anderson, 2009; Bennion *et al.*, 2015b). The choice to include or not include the correlation structure was conducted using the log-likelihood of each model (package "mgcv", Wood, 2016).

Because we hypothesize that local human impact may have change lakes vulnerability to climate variability (Bruel *et al.*, Under Review), we ran the analysis only for the 1900-2010 period in order to get a similar time frame. Indeed the GAM model that we used to calculate the proportion of change linked to climate variability do not consider any potential bistability. As a result, recent climate variability can be hidden by the weight of previous record when climate vulnerability was lower.

### 3.5.3 | RESULTS

PrC performed poorly in summarizing the variability, so the results are not further discussed. Indeed, PrC are best fit for datasets with a single or dominant gradient (e.g. diatoms along eutrophication gradient, Bennion *et al.*, 2015b).

PCA on the other hand offered the advantage to summarise the variability along more than one gradient. Because we were expecting more than one gradient (i.e. eutrophication and climate warming), it is the method we chose in Chapter 6 to quantify the vulnerability.

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# Chapter | 4

# Multiple stable states in a deep lake

# 4 | SEEKING ALTERNATIVE STABLE STATES IN A DEEP LAKE

**Rosalie Bruel(1), Aldo Marchetto(2), Anaëlle Bernard(1), Andrea Lami(2), Pierre Sabatier(3), Victor Frossard(1), Marie-Elodie Perga(1,4)***

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(1) CARRTEL, INRA, Université de Savoie-Mont Blanc, 74200 Thonon-les-Bains, France

(2) CNR-ISE, 28922 Verbania Pallanza, Italy

(3) EDYTEM, Université de Savoie-Mont Blanc, CNRS, 73370, Le Bourget du Lac, France

(4) Current address: Institute of Earth Surface Dynamics, University of Lausanne, CH-1015, Lausanne, Switzerland

*Authors contribution: RB, VF, MEP conceived the study. RB and MEP interpreted the results. RB and PS conceived the age model. AM, AB and RB analyzed the core sub-fossil samples. AL quantified pigments in the sediment. All authors contributed to the writing.*

## 4.1 | ABSTRACT

1. Hysteresis linked to alternative stable states may explain delays in water quality recovery despite reduced nutrient loadings in shallow lakes. Because deep lakes are assumed to be less prone to critical transitions, similar delays are attributed to the confounding effects of additional environmental disturbances, such as climate warming. Herein, we hypothesized that the lack of evidence of nutrient-driven alternative stable states in a deep lake arises from the fact that the nutrient threshold that causes the critical transition is lower than the nutrient threshold in shallow lakes. Thereby, it might have been crossed much earlier in the lake history.
2. To test this hypothesis, we focused on the palaeo-ecological trajectory of Lake Varese, which is a deep, hyper-eutrophicated peri-alpine lake undergoing restoration. Proxies for drivers of ecological state (i.e. total phosphorus – TP – through diatoms and pigments) and ecological responses (cladocera), as well as a repeatable analysis, were used to identify transitions and to distinguish hysteretic delays from those of the ecosystems responding to additional constraints over the past century.
3. Our results suggest spatial heterogeneity in the ecological response. The littoral habitats changed abruptly and prematurely for a low TP threshold, causing a shift that met many criteria of a flickering-type critical transition. Soon after the littoral shift, a striking increase in the lake phosphorous concentration was recorded and drove the pelagic assemblage towards a new state. This transition was abrupt, and the pelagic communities exhibited limited evidence of recovery; however, we found no evidence of hysteresis. Therefore, the modern ecological trajectory of the pelagic communities is currently driven by climate warming.
4. This detailed analysis allowed us to go beyond the general pattern that links ecological responses to drivers and suggest that a non-linear transition following eutrophication can take place in a deep lake synchronously with linear transitions. Instead of triggering a new regime shift, climate warming, to which pelagic habitats are more sensitive than littoral ones, has driven the lake further from its safe operating space.

*Keywords | alternative stable state, early warnings, eutrophication, palaeo-ecology, spatial heterogeneity*

## 4.2 | INTRODUCTION

Because man-made eutrophication has been held up as the most important threat on lake water quality over the last 60 years (Schindler, 2006), primary management actions have consisted of controlling and reducing external nutrient loadings into lakes (Jeppesen, Søndergaard & Liu, 2017). These initiatives have been successful in some cases (Edmondson, 1991), but most of the time, result in incomplete recovery (Sas, 1989) and decades-long delays in lake response (Jeppesen *et al.*, 2005). Delays are manifested either as a weak response of lake nutrient concentrations to decreased nutrient loadings (Larsen, Schults & Malueg, 1981) or limited reinstatement of water transparency despite decreases in lake nutrient concentrations (Anneville *et al.*, 2009). When the latter situation is observed in shallow and unstratified lakes, one hypothesis is related to the hysteretic response of primary producers following a nutrient-driven critical transition (Scheffer *et al.*, 2001; Scheffer & van Nes, 2007).

Shallow lakes have long been archetypal systems for testing regime shift theories (Scheffer *et al.*, 2001; Jackson, 2003; Scheffer & van Nes, 2007), in which the specific feedback mechanisms responsible for alternative turbid and clear-water stable states are mostly tied to water mixing, sediment resuspension and macrophyte interaction with water clarity (reviewed in Hilt, 2015). Because the relative magnitude of all three processes decreases with lake size and depth (Janssen *et al.*, 2014), the stabilizing mechanisms responsible for alternative stable states are generally assumed to be limited in larger, deeper and thermally stratified lakes (Scheffer & van Nes, 2007; Capon *et al.*, 2015), In fact, for lakes, which have a maximum depth that exceeds 10 m (Genkai-Kato & Carpenter, 2005; Hilt *et al.*, 2010; Hilt, 2015), linear or continuous, rather than discontinuous responses to nutrients concentrations are expected (van Nes & Scheffer, 2005; Janssen *et al.*, 2014).

Generally, in deep lakes, the delayed and incomplete recovery of water transparency is regarded as an outcome of additional human disturbances (including climate warming, Jeppesen *et al.*, 2005; Alric *et al.*, 2013; Perga *et al.*, 2015) driving the system to a new ecological trajectory (Battarbee *et al.*, 2005; Bennion *et al.*, 2015b). Indeed, climate change can impact lake ecosystems through several direct and indirect pathways, including a lengthening of the stratification period and enhancement of hypoxia, both promoting P release from the sediment, changes in water level or nutrient loadings, or temperature-induced changes in biotic interactions (Jeppesen *et al.*, 2017).

However, recent studies provided evidence for alternative stable states in relatively deep lakes, with stabilizing mechanisms that varied substantially as compared to shallow lakes. The deep (20 m) Lake Erhai, in China, has undergone a nutrient-driven regime shift in the early 21st century (Wang *et al.*, 2012). Nutrient loadings from agriculture on Lake Erhai watershed increased continuously from 1960 up to 2000, resulting at first in a trend change of primary producers as long as the lake bottom was oxygenated. Twenty years of short-lived changes in the lake level (due to both human and climatic effects) acted as a trigger for bottom hypoxia and recycling of biologically available phosphorus from the upper sediment. Hypolimnetic oxygen depletion has created a positive feedback mechanism from which eutrophication boomed, and the lake shifted to an alternate attractor in 2001. Alternative stable states could also be experimentally triggered in the water column of deep lakes, manipulating top-down pressure (Seekell *et al.*, 2013). This fish-manipulation experiment suggests that in pelagic-dominated lakes, trophic cascades can shift a system from a stable planktivore-dominated state to an alternate piscivore-dominated state (Seekell *et al.*, 2013). Hence, not only regime shifts might be possible in deep lakes, but due to the difference in the mechanisms in play, they could occur also at a much lower nutrient threshold than the one observed in shallow and small lakes (Scheffer & van Nes, 2007; Janse *et al.*, 2008), whereas the range of nutrient concentrations for which two stable states coexist could be narrower (van Nes *et al.*, 2002).

Since the critical transition might have been crossed very early in the lake history, at rather low human disturbance levels and before any historical monitoring, potential hysteresis might be difficult to demonstrate with instrumental data in deep stratified lakes. Instead, because deep lakes are an ideal context for measuring sequential sedimentation, they provide an opportunity for high-resolution palaeo-ecological reconstruction (Perga *et al.*, 2015) allowing to test for early nutrient-driven regime shifts triggering alternative stable states (Wang *et al.*, 2012; Randsalu-Wendrup *et al.*, 2016; Bunting *et al.*, 2016).

We explored the long-term ecological dynamics of Lake Varese (northern Italy), which is a relatively large and deep lake that underwent drastic changes over the course of the 20th century. This lake became hypereutrophic in the 1950s. Phosphorus abatement measures efficiently cut lake nutrient concentrations by a factor 3 at first, reducing them to values more typical of eutrophic status (100 µg $P.L^{-1}$), after which the lake has stabilized despite further management actions (Zaccara *et al.*, 2007). Rare monitoring data provide little observational evidence of ecological recovery of Lake Varese, despite 40 years of nutrient remediation (Zaccara *et al.*, 2007). We aimed at testing whether the delay in the ecological recovery of this deep lake, under a reduction in phosphorous concentrations after hyper-eutrophication, arose from a hysteretic process (the hypothesis of alternative stable states due to an early nutrient driven regime shift) or to the confounding effect of climate warming that has countered remediation measures (climate warming hypothesis). To this end, the ecological state (*sensu* Mac Nally, Albano & Fleishman, 2014) of the lake over the last 170 years has been reconstructed using sub-fossil cladoceran remains, along with the temporal dynamics of dominant environmental forces (Sayer *et al.*, 2010; Alric *et al.*, 2013).

A sudden change in an ecosystem state variable is a necessary, albeit insufficient, condition of regime shift (Andersen *et al.*, 2009; Dakos *et al.*, 2015; Spears *et al.*, 2017). Indeed, an ecosystem state variable responding through a smooth and continuous pressure-status relationship to a strong stepwise change of this driver over time (as, for instance, a sudden increase in phosphorus concentrations or the sudden atmospheric warming observed over Europe in the late 1980s, Woolway *et al.*, 2017) would itself exhibit an abrupt change (Andersen *et al.*, 2009) in the absence of any bistability (Dakos *et al.*, 2015). Therefore, we used a multistep process aimed at testing all three necessary properties of a regime shift (sudden change, threshold-response and bistability, Andersen *et al.*, 2009; Bunting *et al.*, 2016). We also tested whether major abrupt breaks were preceded by a loss of resilience, manifested through increased variance and autocorrelation, i.e., expected signals for critical slowdowns (the recovery rate from small perturbations becomes very slow) and flickering (the system starts jumping back and forth between alternative basins of attraction) preceding a regime shift (Scheffer *et al.*, 2009; Dakos *et al.*, 2012). Finally, the settlement of a new stable regime shall be followed by a lower variability of state variables (Scheffer & van Nes, 2007; Dakos *et al.*, 2015).

## 4.3 | METHODS

### 4.3.1 | STUDY SITE AND CLIMATE

Lake Varese (45°48° N, 08°45° E) is a warm monomictic lake (14.8 $km^2$, $z_{max}$= 26 m) that is located 238 m above sea level in the subalpine region of northwestern Italy (Figure 4.1). The two main tributaries, the Brabbia channel and the Tinella stream, have annual average discharges of $23 \times 10^6$ $m^3$ $year^{-1}$ and $10 \times 10^6$ $m^3$ $year^{-1}$, respectively. The water flows out through one effluent, the Bardello stream, whose annual average discharge is $80.4 \times 10^6$ $m^3$ $year^{-1}$. Lake Varese has a water renewal time of approximately 2 years (Provini, Marchetti & Tartari, 1992). It qualifies as a hollow lake according to the basin shape index (Bi= 2.8; Meybeck, 1995) and, compared to lakes where regime shift studies were tested (van Donk *et al.*, 1993; Scheffer *et al.*, 1993; Seekell *et al.*, 2013), we qualified it as a deep lake. Increased consumerism following the end of World War II (Scrivano, 2005) as well as the mass-immigration of Italians to Milan and the northwestern part of Italy in the 1950s and the 1960s (Foot, 1999) generated important demographic pressure on the region surrounding Lake Varese. Uncontrolled inputs of domestic phosphorus have led to lake hyper-eutrophication since the 1950s (> 400 µg $P.L^{-1}$ in 1975) (Istituto di Ricerca Sulle Acque, 1980), with negative consequences for the local fish populations that have been exploited since 1900. Remediation actions were conducted nationwide to reduce the P load in freshwater based on the first water quality law in 1976 (with successive regulations of a maximal allowed percentage of P in detergent). Subsequent local P abatement measures (a new wastewater treatment plant in 1994) led to a 68 % reduction in the external load, and the lake reached eutrophic status in the late 1990s (117-130 $\mu$g P.L$^{-1}$) (Crosta, 1999) but stabilized thereafter, despite further reductions of inputs. Complementary measures to limit P release from sediment (hypolimnetic water withdrawal and oxygen injection) from 2000-2003 had no better success at reducing TP concentrations. The internal P loads, inherited from the past hyper-eutrophication phase and remobilised from the sediment through bottom hypoxia, might be responsible for maintaining TP concentrations at levels typical of eutrophic status. Again, it is yet unclear whether this resistance to remediation is the result of hysteresis (Genkai-Kato & Carpenter, 2005) or climate warming fostering bottom hypoxia (Jenny *et al.*, 2014).

The climate of the region is subcontinental and temperate, with warm and dry summers and cool and wet winters. The datasets of annual, winter, and summer air temperatures, as well as precipitation, were extracted from the gridded HISTALP dataset (Auer *et al.*, 2007) according to lake geographical coordinates for the time period covered by the sedimentary records (1837-2010). The data show a significant trend in atmospheric temperature over the last 100 years (Mann-Kendall= 0.50, $p < 2.66 .10^{-16}$), with an initial slow increase from 1900 to 1980 (+0.1°C/decade), which was reinforced by a significant shift in the mid-1980s (+1°C in 5 years).

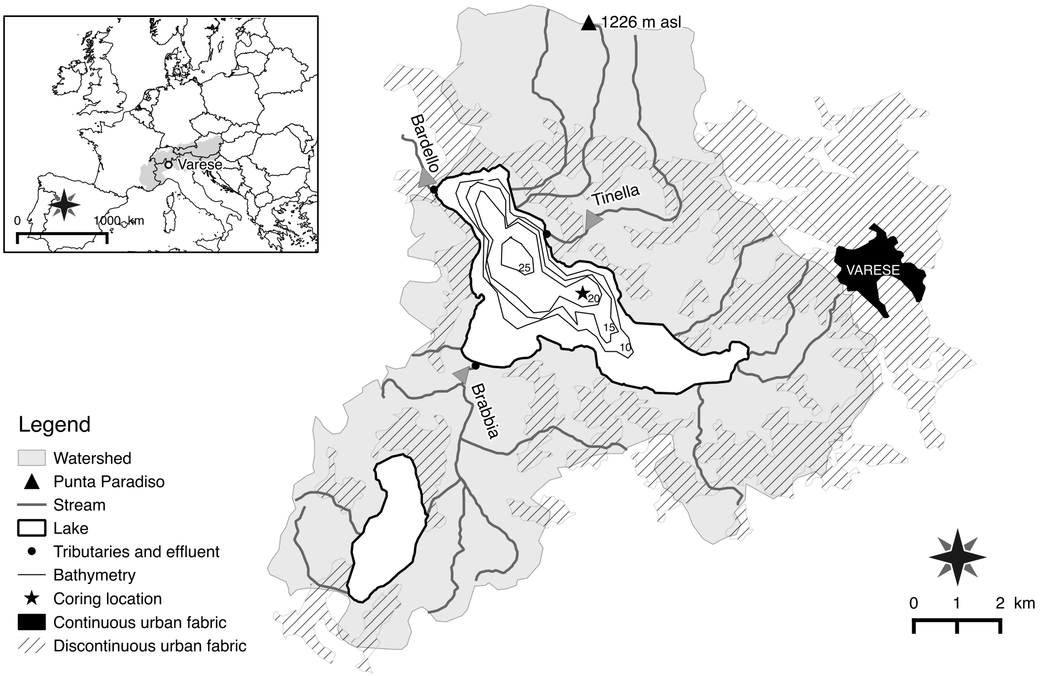

**Figure 4.1 |** Lake Varese catchment.

Delimitation of the urban areas was obtained from the CORINE Land Cover seamless vector database (RELEASE v18_5, 2012).

Such a trend is common to the overall European region (Woolway *et al.*, 2017). A weak, yet significant, decreasing trend in local annual precipitation has been detected (Mann-Kendall= -0.15, $p < 0.004$).

### 4.3.2 | CORING & DATING

A sediment core (VAR 10.10 74 cm long) was collected in 2010 using a gravity corer with a PVC tube from the lake's deepest zone (45°49'51'' N, 8°43'08 E). Half of VAR 10.10 was sliced at a 1-cm interval and was used to count diatoms and cladoceran, as well as to measure pigments. The chronology was based on $^{210}$Pb, $^{226}$Ra, $^{137}$Cs and $^{241}$Am activities measurement using gamma spectrometry, carried out in September 2010 on a reference core (VAR 10.4 89 cm-long). In every 1-cm of the first 28 cm of core VAR 10.4, the ($^{210}$Pb unsupported) excess activities were calculated by subtracting the ($^{226}$Ra-supported) activity from the total ($^{210}$Pb) activity. Lake Varese sediment presents a laminated facies, characteristic of deep water anoxic conditions (Jenny *et al.*, 2013) in their topmost portion. The number of laminae compared with the age model (on VAR 10.4, the dated core) allowed us to confirm that the sediment was annually varved. Varve counting could then be used to validate the age model and to correlate the dates between the VAR 10.4 and VAR 10.10 cores.

### 4.3.3 | INFERRED WATER [TP]

Only sporadic TP measurements were available. The mean total phosphorous (TP) concentrations were reconstructed using diatom and pigment-based inference models. The two proxies were combined because both methods present well-known limitations. On one hand, the diatom responses to perturbation may be delayed (Davidson *et al.*, 2011) and could give seasonally biased results, as diatoms are often most abundant in the spring and autumn (Reynolds, 1984). Therefore, diatom-inferred TP does not necessarily capture changes in TP at low concentrations (Berthon *et al.*, 2014). On the other hand, pigments are known to be sensitive to early changes in pressure (McGowan *et al.*, 2005; Bunting *et al.*, 2016), but they do not reflect TP concentrations when P is no longer a limiting factor, which is the case at very high TP levels. To compensate for the limitations of each of these inference methods, we compiled a composite inferred–TP (I-TP), in which CarI-TP was used until 1946 and DI-TP thereafter, as an independent driver for ecological changes in the analysis. The individuals DI-TP and CarI-TP, such as the validation for I-TP are presented extensively in Chapter 2.

### 4.3.4 | SUBFOSSIL CLADOCERANS

The cladoceran remains were analysed according to Frey (1986). > 400 cladoceran remains were counted and identified per sample (headshields, shells, post-abdomens, post-abdominal claws, mandibles and others) using the Szeroczynska and Sarmaja-Korjonen keys (2007) and an

Olympus BX41 microscope at 100-200 magnification. *Bosmina* were determined to the species level (*B. longirostris*, *E. longispina*, and *E. coregoni*), as well as chydorids, whenever possible. Given their taxonomic complexity, *Daphnia* spp. were identified to the genus level.

### 4.3.5 | STATISTICAL ANALYSIS

Data aggregation and statistical analyses were performed using R version 3.1.2 (2014-10-31) (R Core Team, 2014), as well as the packages cited below. The main changes in the cladoceran community over time were summarized using a multivariate ordination method, comparing a Principal Component Analysis (PCA) and Detrended Correspondence Analysis (DCA) ordinations performances (package "vegan", Oksanen *et al.*, 2016). The DCA explained more variance in the dataset than the PCA and was thereafter selected. We used information summarized in the orthogonal principal components and the known taxa ecological preferences (Hann, 1989; Bjerring *et al.*, 2009) to describe the main changes in the community structure. Change-point analysis (package "changepoints", Killick *et al.*, 2016) was used to estimate the changes in the series mean. Because DCA can spread long or dominant gradients over several ordination axes (Simpson & Birks, 2012), we tested the analysis on several ordination axes. Changes in the mean DCA axes were assessed using the Pruned Exact Linear Time (PELT) method and constrained with a penalty. Lower penalty values occurred when more change points were identified. The penalty was determined with Akaike's information criterion (AIC) and were verified manually by conducting an elbow plot. Bootstrapped series (1000 iterations) were generated from ordination axes using the replacement method to maintain the data structure but by reshuffling the values. The tested null hypothesis was that the random series would result in the same emergence of change points, whereas the alternative hypothesis was that the number of change points resulted from a specific ordination in time. F-density plots before-after the breaks were drawn to identify bimodality in the distribution of the state variable, i.e. potential stable states (cf. Wang *et al.*, 2012).

The relative contribution of changes in TP (assessed from I-TP) and climate (air temperature and mean annual precipitation records) to the dynamics of DCA scores was assessed by using the Generalized Additive Models (GAMs) as in Alric *et al.* (2013). The final GAMs were chosen by computing models using various forcings as covariates, and the best models were chosen following the AIC. Then, the choice of whether to include a correlation structure was made using the log-likelihood of each model (package "mgcv", Wood, 2016). The competing forcing variables and their effects were separated based on the computed contribution that each covariate makes to the fitted model (Simpson & Anderson, 2009). Finally, the DCA scores were plotted against the identified dominant drivers to detect threshold pressure-status relationships and potential bistability (state phase and F-density plots as in Wang *et al.*, 2012).

Theoretical Early Warning Signals (EWS) were sought for the identified transitions, and among the indicators that have been previously proposed, autocorrelation (AR(1)) and variance (SD) were chosen because these two are the most robust for time aggregation, which is typical of palaeo-ecological records (Frossard *et al.*, 2015). The theory behind rising AR(1) is that before an abrupt ecological change, feedbacks will progressively fail to maintain the ecosystem in its current state. When approaching a tipping point, the system will take more time to recover (i.e., return to the centre of the basin of attraction) from disturbances. As a result, wider fluctuations should be mirrored into an increase in SD. EWS were computed (package "earlywarnings", Dakos *et al.*, 2012) using a bandwidth of 5 – 45 % of the dataset length (i.e., 8 to 70 years) to assess the robustness of the output (Spears *et al.*, 2017). The analysis was also performed on a time-series of the residuals (the observed values minus the Local Polynomial Regression Fitting through weighted least squares) and standardized to the square-root of the corresponding period (to account for the irregular time-resolution), as suggested by Carstensen *et al.* (2013), for varying time windows. Significant monotonic trends in AR(1) and SD (on the DCA scores and residuals) preceding the catastrophic transition were tested using Mann-Kendall's rank correlation tests on various window sizes (6 to 15 data points, i.e., ca. 13 to 33 years) to test the robustness of the results. Finally, if an ecosystem entered a new alternative stable state, SD is expected to be low again because the return rates to the new stable state are high again. To test this hypothesis, the average SDs were compared before and after the transitions using a t-test (10 sample windows, i.e., 22 years).

## 4.4 | RESULTS

### 4.4.1 | AGE MODEL

The oldest sediment in the core (from 74 cm to 20 cm) presented a homogeneous deposit that was lighter below 29 cm and darker above. The most recent 20 cm of the core was silty-clay finely laminated sediment (1 mm-thick), with alternatively yellow to dark grey layers, and the thickness of the laminae decreased upward. The $^{210}Pb_{ex}$ ($^{210}Pb$ unsupported excess) activity decreased logarithmically with two distinct linear trends before/after the 8 cm depth (Figure 4.2). The constant flux from the constant sedimentation rate (CFCS) model (Krishnaswamy *et al.*, 1971) was applied to the two parts of the profile. The levels of $^{210}Pb_{ex}$ represented mean accumulation rates of 0.48 ± 0.06 cm yr$^{-1}$ ($r^{2=}$ 0.837) between depths of 28 and 8 cm and 0.29 ± 0.04 cm yr$^{-1}$ ($r^2$= 0.927) in the upper 8 cm of the core (Figure 4.2), i.e., approximately 40 % lower than in the rest of the core. Caesium peaks (typical for the 1986 Chernobyl disaster and

1963 maximum radionuclide fallout from atmospheric nuclear tests) were detected at 7.5 cm and between 19.5 and 21.5 cm, with a maximum at 19.5 cm, whereas the $^{241}$Am maximum (a tracer of the 1963 maximum radionuclide fallout) was only detected at the 19.5 cm depth and was thus associated with the deepest of the two $^{137}$Cs peaks (Appleby *et al.*, 1991). Artificial radionuclide data thereby confirmed the sedimentation rates computed from the CFCS $^{210}Pb_{ex}$ age model. Varve counting over the first 20 cm (dated at 1960) further confirmed this age model and allowed date correlation of the two cores. Unfortunately, short-lived radionuclides were not measured over the whole sediment core, and the deepest dated layer corresponded to 1941 +/- 10 years AD at 29 cm. Below 28 cm, the dating was based on extrapolation of the lower part the CFCS age model. Sedimentary data (LOI, water content) did not present any significant variations below 20 cm depth, supporting a rather constant mean sedimentation rate over the lower part of this core. Under this postulate, the VAR10.4 core covers the 1816 (± 26) - 2010 time-period, and VAR 10.10, used for the biological analysis, covers the 1837 (± 22) - 2010 time-period. However, throughout the manuscript, the age model below 1940 was taken with caution and the main changes highlighted in this study occurred after 1940.

## 4.4.2 | INFERRED TOTAL PHOSPHORUS

I-TP (Figure 4.3) represents the status before eutrophication corresponded to a mesotrophic lake (I-TP < 15 µg TP.L$^{-1}$). I-TP exhibited a slight increase as early as the 1870s and reached 25 µg TP.L$^{-1}$ just before World War II. Between 1946 and 1948, I-TP increased abruptly from ca. 25 µg TP.L$^{-1}$ to >200 µg P.L$^{-1}$. This abrupt change was consistent for both pigment-inferred and

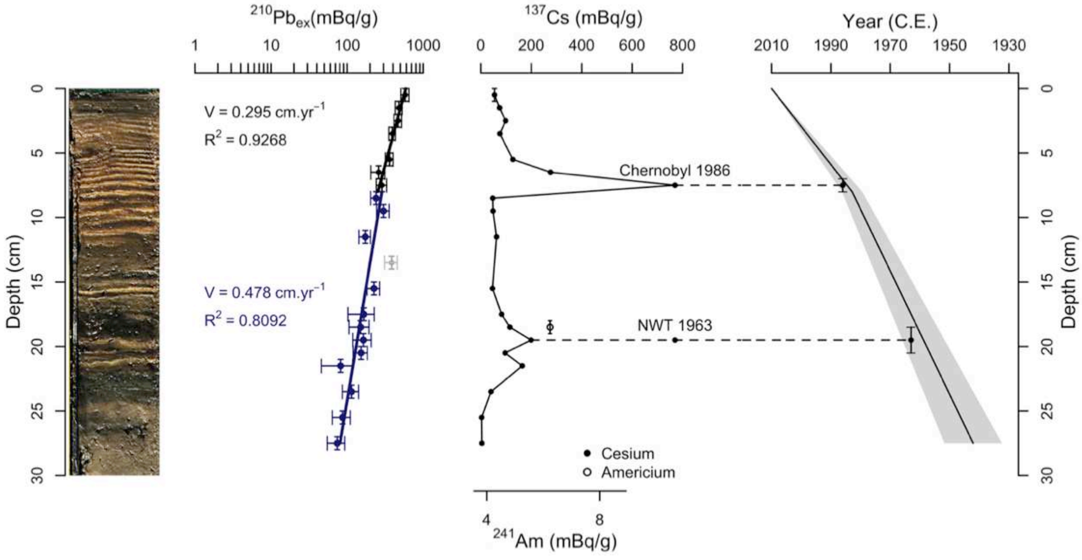

**Figure 4.2 I** VAR10.4, reference cores for dating.

From left to right: photography, $^{210}Pb_{excess}$ activity, $^{137}$Cs activity, $^{241}$Am activity, and the age model for the upper 30 cm with uncertainties. The $^{210}Pb_{ex}$ activity point in grey was not included in the sedimentation rate calculation because the low counting time was too low and led to large uncertainties at 1 σ. NWT stands for Nuclear Weapons Testing.

diatom-inferred TP. I-TP remained high, oscillating between 200-300 µg TP.L$^{-1}$ until the early 1980's. Thereafter, I-TP decreased continually from >300 µg TP.L$^{-1}$ down to 75-100 µg TP.L$^{-1}$ in the most recent samples, which is consistent with currently monitored values.

### 4.4.3 | MAJOR DYNAMICS WITHIN THE ECOLOGICAL PROXY

The length of DCA axis 1 was greater than the length of axis 3 (1.98 vs. 1.30 SD), which indicates that DCA adequately summarized the information in the dataset. Because the first axis was still short and two-dimensional plots are often necessary to convey most of the complex data structure (Wartenberg, Ferson & Rohlf, 1987), the second axis was included in the analysis. The two first axes accounted for 73 % of the total variance in the cladoceran community (Figure 4.3). DCA1 (46 %) essentially accounted for the dominant changes in pelagic species, with the low scores on axis 1 indicating an important contribution of *Chydorus sphaericus* (loadings < 0.4) and *Eubosmina sp.* (loadings < 1.0) to the assemblage, whereas high scores were correlated with an important contribution of *Daphnia* spp. (loadings > 1). DCA2 (27 %) accounted for the changes in the littoral communities, such as for the littoral to pelagic ratios; the low values on axis 2 were correlated with the macrophyte-associated species *R. falcata*, *P. nigra* and P. *truncatus* and Eurycercinae (loadings < 0.5), and the highest values were correlated with greater abundance of *Eubosmina sp.*

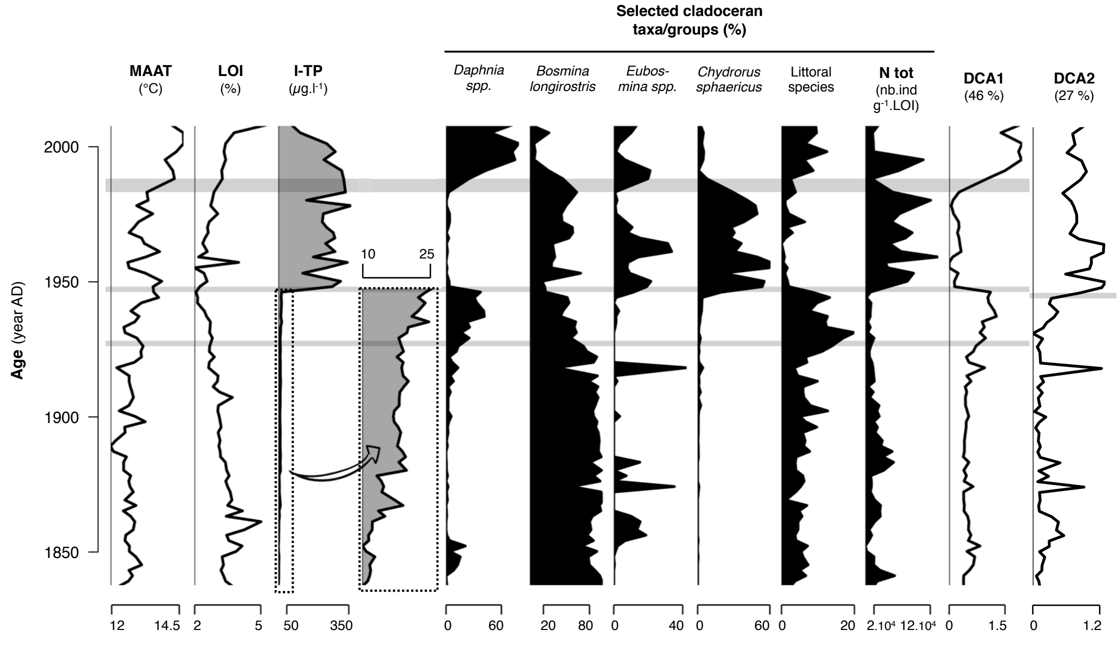

**Figure 4.3 I** Palaeostratigraphy of Lake Varese cladoceran communities from 1837 to 2008.

Core descriptor (LOI), environmental parameters (MAAT: Mean Annual Air Temperature (Auer et al., 2007) and I-TP: Inferred Total Phosphorus), selected cladoceran taxa/groups (units: fluxes (remains cm$^2$.yr$^{-1}$)), and selected axes of DCAs for the total cladoceran assemblage. The horizontal grey areas correspond to the detected transitions.

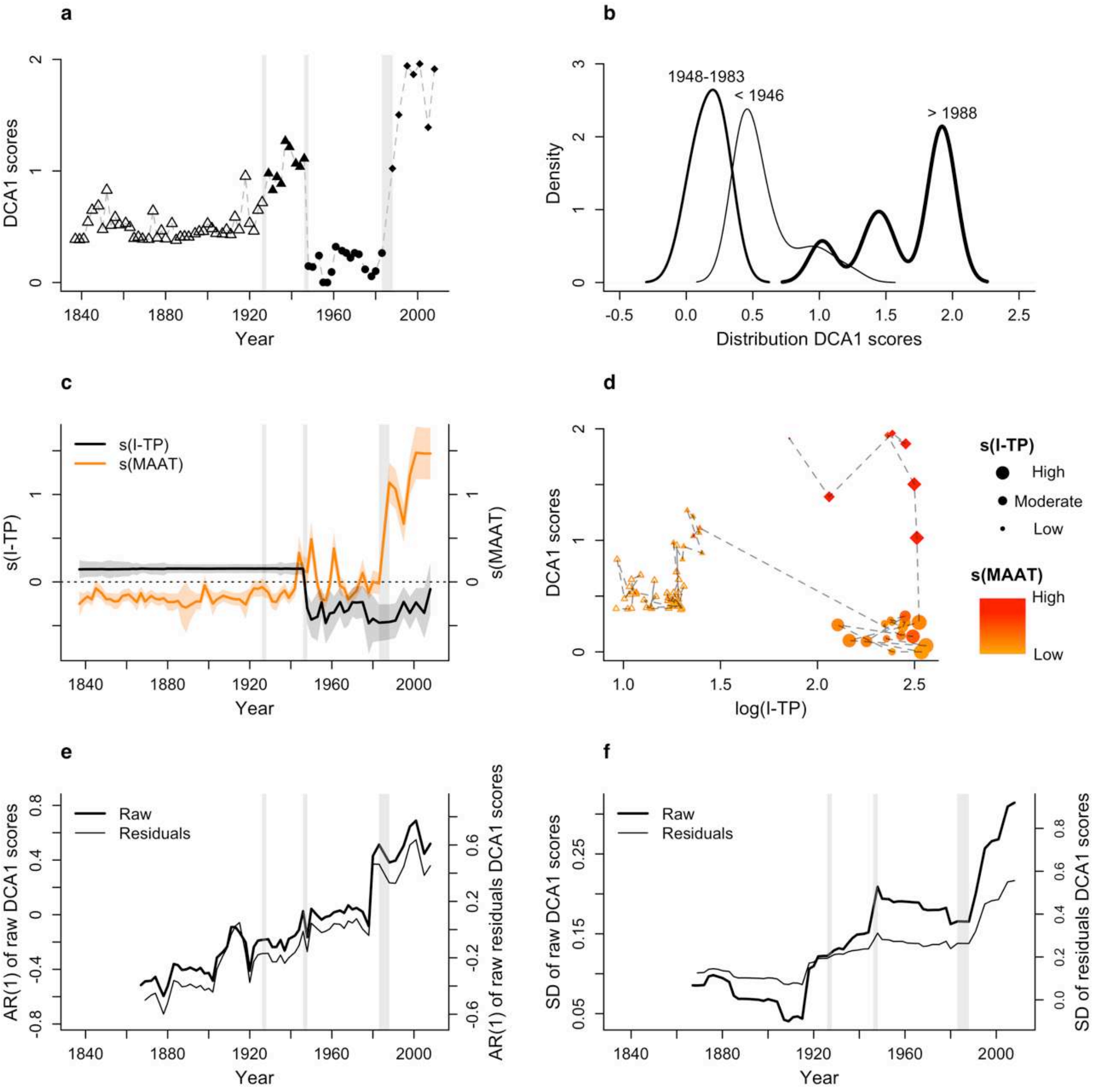

**Figure 4.4 I** Diagnostic of stable states on DCA1.

(a) DCA1. (b) Probability density functions (Gaussian kernel density estimation bandwidth= 0.1) for the periods delimited by the abrupt transitions; i.e., 1946 / 1948 and 1983 / 1988. (c) The temporal contribution of I-TP (s(I-TP), black) and MAAT (s(MAAT), orange) to DCA1 with approximately 95 % pointwise confidence intervals to the contribution. Where the band includes the dashed zero line, the contribution of the covariate is not statistically significantly different from the intercept. (d) Response/Forcing relationship of DCA1/I-TP with I-TP concentration (common logarithm scale). Dots size reflects the contribution of I-TP (s(I-TP) to the assemblage for a given period. Dots colour reflects the contribution of MAAT (s(MAAT)) to the assemblage for a given period. The (e) and (f) are Early Warning Signal (EWS) indicators. (e) Evolution of autocorrelation (AR(1)) and (f) variance (SD). AR(1) and SD were calculated for raw DCA scores on axis 1 (thick line) and its standardized residuals (thin line) with a moving window of 20. The different points in (a) and (d) and (g) reflect the periods between transitions, as detected by the Change-point Analysis: open triangles, 1837-1926; closed triangle, 1928-1946; closed circle, 1948-1983; and open circle, 1983-2008. In (a), (c), (e) and (f), the vertical grey areas correspond to the detected transitions.

### 4.4.4 | NATURE, DRIVERS AND EWS FOR THE BREAKS DETECTED ON CLADOCERAN ASSEMBLAGES

The change-points analysis revealed three dates of significant breaks in DCA1 scores: 1926 / 1928, 1946 / 1948 and 1983 / 1988. There was only one break in the DCA2 that was dated in 1944 / 1946 (Figure 4.3), i.e., one data point earlier than the second one detected on axis 1 (Figure 4.3). The same change-point analysis was conducted on the bootstrapped series of DCA1 and DCA2 with 1000 iterations, indicating an average of 0.165 and 0.006 change points, respectively, indicating that the number of transitions detected was not the result of chance but, instead, of a specific ordination in time.

On DCA1 (Figure 4.4 a), the first transition of the total cladoceran community in 1926 / 1928 corresponded to a smooth increase in the DCA1 scores as I-TP went from < 20 µg P.L$^{-1}$ to > 20 µg P.L$^{-1}$ during a transient warming period. This gradual transition was driven by a progressively higher contribution of *Daphnia* spp. to the total assemblage (from 1 % to 18 %) to the detriment of *Bosmina* sp. and a relatively higher representation of littoral habitats within the total cladoceran assemblage. The second transition (1946 / 1948) signalled a deep reorganization of the cladoceran pelagic community structure. The sudden increase of I-TP between 25 and >200 µg P.L$^{-1}$ coincided with the disappearance of *Daphnia* spp., replacement by *Eubosmina sp.* and overall dominance by *C. sphaericus*, with DCA1 scores close to 0. The latest transition on DCA1 was dated between 1983 / 1988. It marked the unprecedented dominance by *Daphnia* spp. within a few years (68 % of the total assemblage), and the appearance of littoral yet ubiquitous cladoceran species (*Alona* spp., mainly *Alona rectangula*, *Alona affinis*, and *Alona intermedia*) that differed from pre-eutrophication assemblages. The probability density functions (Figure 4.4 b) indicated that the distribution of DCA1 scores between the pre-1946 and post-1948 time-periods overlapped until the 1983 / 1988 break, after which the scores were very distinctive. The final GAM for DCA1 (

Table 4.1, Figure 4.4 c, deviance explained 71.2 %), chosen according to the AIC computation, included a significant smooth term for I-TP ($p = 6.93.10^{-6}$) and the mean annual air temperature (MAAT, $p < 2.10^{-16}$). A correlation structure for the model errors was not supported by a likelihood ratio test, and the two models (with and without the correlation structure) provided effectively the same fit for the observed data. Therefore, the simplest model was retained. Both fitted relationships between DCA1 scores and covariates were nonlinear (EDF= 4.09 and 3.92 for I-TP and MAAT, respectively), with threshold values for which contributions changed signs. I-TP contributed to pushing the DCA1 scores from positive to negative values for inferred concentrations ranging between 50-100 µg P.L$^{-1}$, whereas MAAT essentially contributed to increasing DCA1 above MAAT > 13.7°C. The 1926 / 1928 smooth transition corresponded to a transient positive contribution of MAAT, whereas the 1946 / 1948 transition matched an important shift in s(I-TP) from positive to strongly negative values, supporting the theory that nutrients were by far the dominant trigger of such the abrupt mid-20th century transition (Figure 4.4 c). The GAM run for the 1000 bootstrapped values of I-TP indicated that the contribution of I-TP was significant for the 5-95 % confidence interval for all I-TP (Chapter 2). In turn, MAAT was the clear driver of the 1983 / 1988 transition, and Lake Varese clearly exhibited a strong response to the climatic regime shift characterized in Europe in the 1980s by Woolway *et al.* (2017) (+1°C in 5 years). Interestingly, over the period depicted by the sediments, I-TP and MAAT exhibited antagonistic effects on the DCA1 scores.

The DCA1 scores over the most recent period were significantly different from those observed 50 years ago for similar I-TP values (Figure 4.4 c), but these differences in the reversal trajectory were attributed to the significant contribution of MAAT over the last 30 years. The phase-space plot between DCA1 scores and MAAT also suggested a threshold relationship linking forcing to the response (Figure 4.4 d). The values of EWS were linked to the window chosen for the computation (Chapter 2) as well as to the window of calculation for the Mann-Kendall trend test. However, whatever the computation method, the variance and autocorrelation of DCA1 scores increased along all of the records. Therefore, even though the 1946 / 1948 transition was preceded by a rise in SD and AR(1), no stabilization or decreased variance occurred after the transition (Table 4.2, Figure 4.4 f).

Detrended records of cladoceran composition (DCA2, Figure 4.5 a) before and after the 1944 / 1946 transition are clustered within two different groups. Until 1944, the DCA2 scores were <0.6, except for two outliers above 0.8 in ca. 1897 and ca. 1916. This corresponds to an assemblage with a rich littoral diversity. From 1946, the scores jumped above 0.8, highlighting the loss of the littoral diversity and thriving *Eubosmina sp.*. The final GAM on DCA2 (

Table 4.1, Figure 4.5 b, deviance explained= 62.8 %) selected a non-linear smooth term only for I-TP ($p < 2.10^{-16}$), and the likelihood ratio test rejected a correlation structure. The fitted relationship with I-TP in DCA2 was nonlinear (EDF= 2.41), with 24-25 µg $P.L^{-1}$ threshold values for which the contributions switched from negative to positive. DCA2 captured the nutrient-driven changes in the cladoceran community composition, one data-point earlier than the actual sudden shift in I-TP (and thereby DCA1), through the loss of macrophyte-associated species. Because all sedimentary analyses were conducted on the same half core, this delay is meaningful and independent from potential inaccuracies in the age model. Altogether, the results strengthened the information from DCA1, namely, that the mid-1940s transition was nutrient driven and favoured *Eubosmina* sp. over littoral diversity. The probability density functions (Figure 4.5 b) pointed to a segregated distribution of DCA2 scores before and after the mid-1940s transition.

**Table 4.1 I** Summary for the final GAMs fitted to variables scores for DCA axes (performed on the cladoceran assemblage).

GAM: General Additive Models, without correlation structure, as selected by log-likelihood ratio test; I-TP: Inferred Total-Phosphorus; MAAT: Mean Annual Air Temperature; edf: effective degrees of freedom for the regression spline; Ref.df: reference degrees of freedom used to compute the p-value; F: F-statistics; p-value: associated probabilities; Res.dev (% explained): deviance is a measure of residual variation around the final GAM models analogous to the sum of square in linear regression.

| Variable | Model | Covariate | EDF | Ref.df | *F* | *p*-value | Res.dev (% explained) | Threshold |
|---|---|---|---|---|---|---|---|---|
| DCA1 (46 %) | GAM | s(I-TP) | 4.087 | 5.020 | 7.671 | $6.93 \times 10^{-06}$ | | 50-100 $\mu$g P.L$^{-1}$ |
| | | s(MAAT) | 3.918 | 4.836 | 26.060 | $< 2 \times 10^{-16}$ | | 13.1-13.7 °C |
| | | **TOTAL** | **9.000** | | | | **71.2** | |
| DCA2 (27 %) | GAM | s(I-TP) | 2.414 | 2.961 | 39.760 | $< 2 \times 10^{-16}$ | | 24-25 $\mu$g P.L$^{-1}$ |
| | | **TOTAL** | **3.410** | | | | **62.8** | |

**Table 4.2 I** Diagnostic for early warning signals on DCA1 and DCA2.

Summary of the Kendall rank correlation coefficients (tau, calculated for a sample of 10 values before the break) and t-tests for comparisons of means (calculated for 10 points before and after the breaks – only 6 points after the 1983 / 1988 transition) with corresponding p-values obtained from the tests on autocorrelation at the first lag (AR(1)) and standard deviation (SD) calculated for DCA1 and DCA2 scores and their residuals for each break, identified using the Change-point Analysis method. Significant p-values are in bold. Significant increases of AR(1) and SD before the break (tau>0 and p< 0.05) were considered as EWS and are identified with an asterisks in the table. New alternative stable states following transitions implied lower SD (t<0 and p< 0.05), tested through t-tests and identified with two asterisks in the table.

| Axis | Breaks | Test parameter | DCA scores | | | Standardized residuals of DCA scores | | |
|---|---|---|---|---|---|---|---|---|
| | | | ***AR(1)*** | ***SD*** | | ***AR(1)*** | ***SD*** | |
| | | | *Kendall* | *Kendall* | *t-test* | *Kendall* | *Kendall* | *t-test* |
| DCA1 | 1946 / 1948 | Test | 0.590 | 0.974 | 8.906 | 0.795 | 0.897 | 3.102 |
| | | p-value | **0.006*** | **<0.001*** | **<0.001** | **<0.001*** | **<0.001*** | **<0.001** |
| | 1983 / 1988 | Test | 0.538 | -0.718 | 3.364 | -0.436 | -0.564 | 2.982 |
| | | p-value | **0.012*** | **<0.001** | **0.007** | **0.044** | **0.008** | **0.0134** |
| DCA2 | 1944 / 1946 | Test | 0.462 | 0.769 | -4.114 | 0.897 | 1.000 | -4.7735 |
| | | p-value | **0.033*** | **<0.001*** | **<0.001**** | **<0.001*** | **<0.001*** | **<0.001**** |

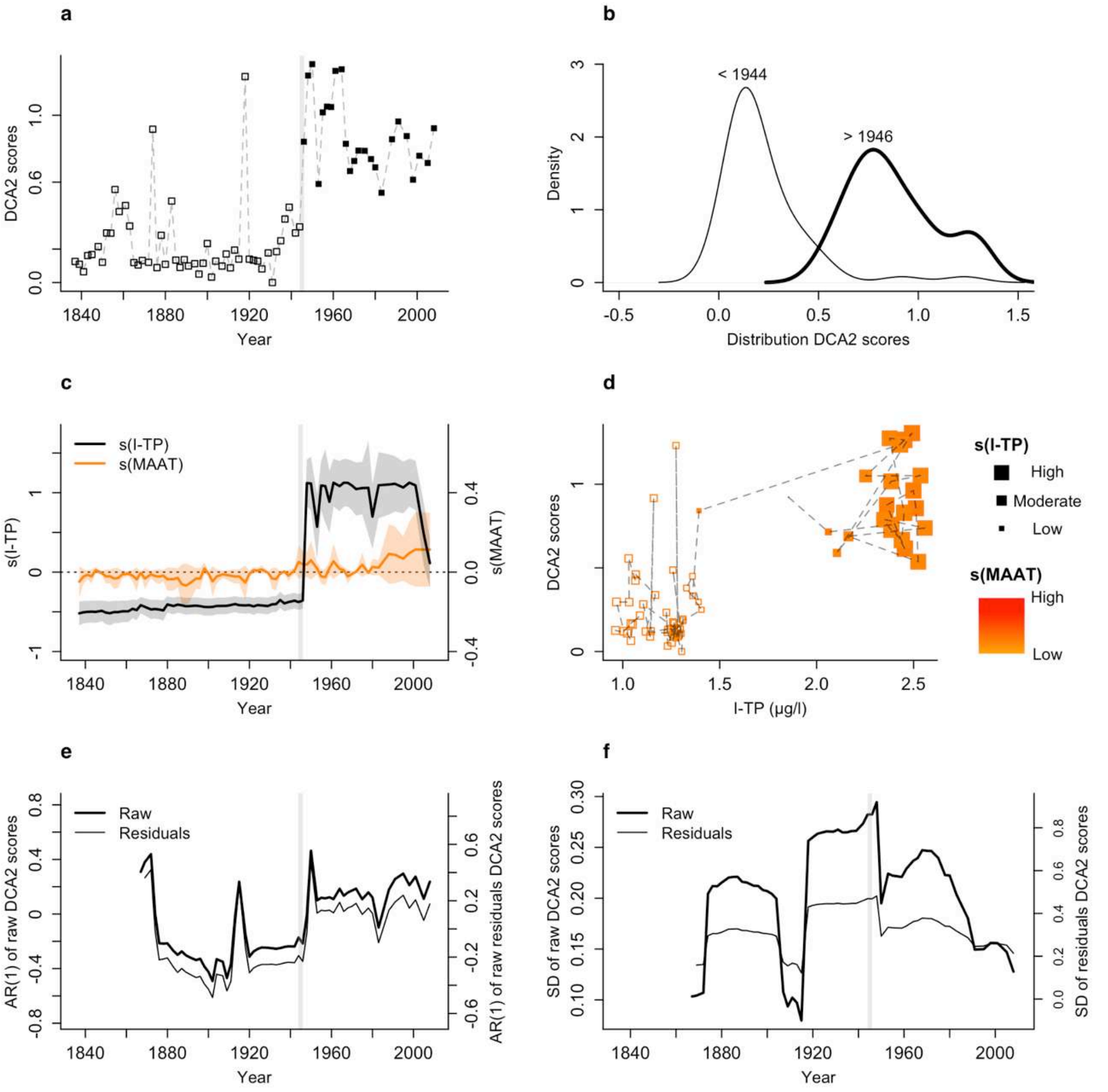

**Figure 4.5 I** Diagnostic of stable states on DCA2.

(a) DCA2. (b) Probability density functions (Gaussian kernel density estimation bandwidth= 0.1) for the periods delimited by the abrupt transitions; i.e., 1946 / 1948 and 1983 / 1988. (c) The temporal contribution of I-TP (s(I-TP), black) and MAAT (s(MAAT), orange) to DCA1 with approximately 95 % pointwise confidence intervals to the contribution. Where the band includes the dashed zero line, the contribution of the covariate was not statistically significantly different from the intercept. (d) Response/Forcing relationship of DCA2/I-TP with I-TP concentration (common logarithm scale). Dots size reflects the contribution of I-TP (s(I-TP) to the assemblage for a given period. Dots colour reflects the contribution of MAAT (s(MAAT)) to the assemblage for a given period i.e. stable null contribution on DCA2. The (e) and (f) are Early Warning Signal (EWS) indicators. (e) Evolution of autocorrelation (AR(1)) and (f) variance (SD). AR(1) and SD were calculated for raw DCA scores on axis 2 (thick line) and its standardized residuals (thin line) with a moving window of 20. The different points in (a) and (d) and (g) reflect the periods between transitions as detected by the Change-point Analysis: open square, 1837-1944, closed squares, 1946-2008. In (a), (c), (e) and (f), the vertical grey areas correspond to the detected transitions.

The phase-space plot between DCA2 scores and I-TP (Figure 4.5 d) outlined two clusters for a I-TP threshold of approximately 24-25 µg $P.L^{-1}$. Because I-TP has not crossed the initial threshold (25 µg $P.L^{-1}$), we do not have evidence of the existence of two alternative cladoceran states for an overlapping range of I-TP. SD and AR(1) of the DCA2 scores significantly increased over the 10 to 20 years preceding the 1944 / 1946 critical transition (Table 4.2). Furthermore, the variance in the following state was significantly lower than before the transition (Table 4.2, Figure 4.5 f). Under the hypothesis that the two modes in the distribution of the DCA2 scores (Figure 4.5 b) represent the attraction basins for the two stable states, then the 3 transient outbreaks in DCA2 scores <1944 (in 1856, 1874 and 1918, Figure 4.5 a) can be interpreted as a flickering signal; i.e., the system started shifting from one stable state to another. This is highly plausible considering the low TP threshold found (<25 µg $P.L^{-1}$).

## 4.5 | DISCUSSION

Lake Varese underwent three ecological transitions over the past 170 years. While the first one in the 1920s was gradual, the two following ones entirely restructured the cladoceran assemblage: once in the mid-1940s, and, most recently, in the 1980s. DCA allowed decomposition of the changes in communities into pelagic and littoral components. The timing, drivers and dynamics of the transitions were different between these two components, further suggesting the possibility of spatial heterogeneity in the susceptibility of regime shift in this stratified lake (Scheffer & van Nes, 2007). The results on DCA1 underlined the necessity to consider the possibility of multi-forcings acting on ecological dynamics when evaluating restoration trajectories (e.g., Bennion *et al.*, 2015b). DCA2 instead gave a more precise picture of the nutrient-driven changes.

### 4.5.1 | CHANGES IN THE PELAGIC COMMUNITY

Unsurprisingly for a rather deep lake, the sub-fossil records archived in the deep sediment core essentially reflected the changes in the pelagic (*Daphnia* spp., *Eubosmina* sp. and *Bosmina* sp.) and opportunist pelagic (*C. sphaericus*, de Bernardi *et al.*, 1990; Manca & Comoli, 1995) cladoceran species (95 % of the total assemblage). Therefore, the temporal variability of the ecological state of the pelagic, dominant habitat of Lake Varese was well captured in DCA1, and the percent of explained variability accounted for by the GAM supports the hypothesis that changes in lake phosphorus concentrations and atmospheric temperatures were the dominant drivers of its dynamics.

The sudden mid-1940s shift in DCA1 scores coincided with the rapid increase in lake phosphorus concentrations, which, according to I-TP, jumped from 25 to >200 µg $P.L^{-1}$ within a couple of years. Consistently, GAM identified I-TP as the trigger of this sudden change. Yet, this strong, stepwise change occurred after 20 years of gradual rearrangements of the cladoceran community structure. Before 1926, *Bosmina longirostris* was the dominant pelagic species, but it was progressively supplanted by *Daphnia* spp. between 1926 and 1946. During this time-period, the sediment content in the carotenoid pigments had already started to increase, suggesting an early and slow eutrophication phase. Furthermore, this time-period also coincided with a transient overall global warming phase, between 1920 and 1945 (Jenny *et al.*, 2016). The GAM attributed this early and gradual rearrangement in the pelagic cladoceran community to atmospheric warming rather than to the earlier increase in I-TP. It is actually more plausible that both factors occurred simultaneously and interacted in this substitution of *Bosmina* sp. by *Daphnia* spp. The mechanisms by which increased TP could foster such a transition are rather direct and relate to *Daphnia* stoichiometric requirements. *Daphnia* spp. is more susceptible to phosphorus limitations than *Bosmina* species (Schulz & Sterner, 1999), making them highly sensitive to increasing TP concentrations in lake waters (Alric *et al.*, 2013). The outcome of the competition between *Daphnia* and *Bosmina* species becomes beneficial to the former when P limitation is released (Schulz & Sterner, 1999; Alric *et al.*, 2013). If the community effects of warming were consistent between this transient warming phase and the most recent warming period (post-1988), i.e., favouring *Daphnia* spp. over small-bodied cladoceran species, they are somewhat in contradiction with those more traditionally expected species. The direct and indirect consequences of a warmer climate, such as warming water, potentially higher abundance of filamentous algae, and subsequent increased fish predation pressure, are all expected to favour *Bosmina* or *Eubosmina* sp. over *Daphnia* spp. (Jeppesen *et al.*, 2007; Alric *et al.*, 2013). However, there are alternative mechanisms that would favour *Daphnia* spp. over small-bodied cladocerans in a warmer climate. For instance, a longer stratification of the lake, promoted by warmer air temperatures, would extend the period when Daphniidae can seek refuge from fish predators in the hypolimnion (Manca *et al.*, 2007). Furthermore, Daphniidae can benefit from accentuated growth at the onset of the season when predation pressure is still low (Boersma, van Tongeren & Mooij, 1996). TP concentrations in pelagic waters could also indirectly depend on atmospheric temperatures if P transport from the catchment, remobilization from the sediment or evapotranspiration and inflows are modified due to climate variability (Jeppesen *et al.*, 2009). However, beyond these speculations, the meaningful message is that the ecological outcome of a warmer climate on species assemblages is highly idiosyncratic. Depending on the geomorphology, exposure or trophic level, climate warming can be detrimental to a species in one lake, but beneficial to the same one in a neighbouring system (Alric *et al.*, 2013; Li *et al.*, 2016).

While *Daphnia* spp. thrived during the earlier eutrophication phases, they became rare within a couple of years as the lake turned hypereutrophic. At these high concentrations, P does not favour *Daphnia* spp. anymore, as the presence of filamentous algae or cyanobacteria typical of hypereutrophic conditions interfere with their feeding apparatus and therefore, their ability to feed (Gliwicz, 1990; DeMott, Gulati & Van Donk, 2001). Alternatively, the *Chydorus sphaericus* that dominated the hypereutrophic assemblage is one of the only cladoceran species able to cope with algal filaments (Tõnno *et al.*, 2016). The growth of this species has been related to important cyanobacterial blooms on which opportunistic *C. sphaericus* attach (de Bernardi *et al.*, 1990) and feed (Manca & Comoli, 1995). The substitution of *Bosmina* by *Eubosmina* sp. shall instead be explained as a top-down mediated secondary consequence of hyper-eutrophication (Perga *et al.*, 2010). Lake bottom anoxia, which appeared during this phase, has triggered massive fish mortality since the 1960s (Ceccuzzi, 2003, 2008; Provincia di Varese, 2010), benefitting *Eubosmina* sp. because they are better competitors than *Bosmina longirostris* when fish are absent (Brooks & Dodson, 1965).

Therefore, the succession in cladoceran pelagic assemblages during Lake Varese hyper-eutrophication is in line with nutrient-driven changes that have already been documented in literature (Alric *et al.*, 2013; Li *et al.*, 2016); however, the speed at which this shift occurred is stunning, especially for a large lake. There was considerable interest in testing whether such a dramatic shift evidenced a critical transition between alternative stable states. The relationship between I-TP and pelagic cladoceran changes might not be linear, but the exact shape of the relationship was actually difficult to accurately define, due to the steep and synchronous change in both the response and the driver. However, a threshold effect is quite likely, since the DCA1 scores remained quite stable until the mid-1980s, despite substantial variability in I-TP between 200 and 300 μg $P.L^{-1}$. However, beyond 200 μg $P.L^{-1}$, nitrogen instead of phosphorus is the limiting nutrient of phytoplankton growth (Seip, 1994), thereby explaining why the amount of pelagic cladoceran changes above this threshold did not scale to I-TP. If re-oligotrophication did not take the reciprocal path, this apparent bistability could be firmly attributed to the additional impact of climate warming on the cladoceran pelagic communities. Consequently, the suddenness of the 1946 shift in the pelagic community structure arose from both a strong stepwise change in I-TP and a threshold-type pressure-response relationship that tied cladoceran community structure to I-TP. The criteria for loss of resilience and true bistability were not met, as the variance kept increasing after the transition as it did over the preceding 3 decades. Altogether, our analysis did not provide any evidence of a nutrient-driven regime shift generating a hysteretic response in pelagic ecological communities causing decreased nutrient concentrations.

The mid-1980s transition observed for the pelagic assemblages has been clearly driven by warming, although a return of decreasing nutrient concentrations below the 150 µg P.L$^{-1}$ threshold could potentially interact in the responses. The F-density plot highlighted that the recent most ecological status of the pelagic communities does not compare to any situation observed over the last century and suggested that pelagic communities in a still-nutrient rich deep lake are highly sensitive to climate warming (Alric *et al.*, 2013; Berthon *et al.*, 2014; Savichtcheva *et al.*, 2015). A study conducted on the large but shallow Lake Winnipeg, using an overall reasoning similar to ours, indicated that even if atmospheric warming had been quite pronounced in that region, the nutrient effects override the climate effect in controlling the lake planktonic trajectory. As such, lake depth, along with nutrient concentrations, appears to be an important regulator of the sensitivity of planktonic communities to climate warming. Warming reinforces the strength and duration of thermal stratification in deep and stratified lakes (Adrian *et al.*, 2009; Kraemer *et al.*, 2015). In P-rich lakes, these hydrodynamic changes increasingly cause vertical heterogeneity of P and inflating changes in plankton communities (Pomati *et al.*, 2017) when the lake is sufficiently rich. However, and contrary to previous observations of eutrophicated lakes, warming did not reinforce hyper-eutrophication symptoms in Lake Varese (Moss *et al.*, 2011). The re-emergence of *Daphnia* spp. and rarefaction of *C. sphaericus* suggested a lower contribution of filamentous algae to phytoplankton populations. A bottom-up scenario that was favourable to *Eubosmina sp.* was replaced by climate as a driving factor favouring *Leptodora kindtii* and *Daphnia* spp. These two species are now the principal components of the pelagic community, and *B. longirostris* does not have a competitive advantage in recovering its prior-eutrophication habitat. This new balance in the pelagic community suggests a currently low fish fauna pressure from predation (Ceccuzzi *et al.*, 2011). Altogether, the climate-warming hypothesis explained the delay in recovery of the pelagic habitat, which is dominant in the deep Lake Varese.

If the warming-driven reorganization of the pelagic cladoceran communities in the 1980s occurred suddenly, its dynamic was consistent with the observed shift in atmospheric temperature over Europe (a 1°C increase within 5 years, between 1983-1988). Although climate might have triggered a regime shift, this situation, of a strong stepwise change in the driver, was not expected to generate EWS (Dakos *et al.*, 2015). In fact, no sign of resilience loss was observed (Table 4.2). The results also suggest that the driver-response relationship was non-linear, with a threshold value at 13.7°C, but the paucity of data points after the transition limited the confidence of the fit. Lastly, atmospheric temperatures obeyed a monotonic increasing trend, offering no opportunity to test for bistability. Although climate warming has been shown to trigger diatom regime shifts in lakes (Smol *et al.*, 2005), other examples are rare. The time-resolution of palaeo-ecological studies might limit our ability to evaluate whether recent climate warming is prompt in triggering regime shifts in deep lakes, and we ended up in conjectures either confirming or disproving this hypothesis. Interestingly, the variance of DCA1 scores increased throughout the record, independently from the potential bias due to uneven time resolution (the same trend was observed on the calculated residuals, accounting for the change in time-resolution). Increased variance can be interpreted as a loss of resilience in the ecosystem under pressure (Dakos *et al.*, 2015), but this also comes with a weakened predictability of the further evolution of the lake (Cottingham, Rusak & Leavitt, 2000; Bunting *et al.*, 2016). Therefore, even though the lake's main pelagic habitat might not be undergoing hysteresis, its management could face some 'surprise effects'.

### 4.5.2 | CHANGES IN THE LITTORAL COMMUNITY

The question of alternative states in lakes is usually dealt with from a spatially averaged perspective, under the tacit assumption that changes occur synchronously lakewide. However, instead, regime shift could be restricted to certain habitats, or could occur at different paces, depending on habitats (van Nes & Scheffer, 2005; Scheffer & van Nes, 2007; Janssen *et al.*, 2017). Herein, the littoral assemblages were well recorded in the sediment archives despite the lake shape, depth and location of the coring site, thereby allowing to separately consider the dynamics of littoral versus pelagic habitats. DCA2 mirrored both the temporal changes in the littoral species, along with the ratio of benthic versus planktonic species. These changes contributed significantly to the lake-wide modifications of cladoceran assemblages (27 % of the total variability explained on DCA2). DCA2 suffered only one transition in 1944 / 1946, during which a diverse littoral community, made of species indicative of a productive and macrophyte-rich littoral zone, such as *Graptoleberis testudinaria*, *Alonella excisa*, *Alonella nana* and *Rynchotalona falcata* (Hann, 1989; Bjerring *et al.*, 2009), became extinct. Although this transition was unequivocally attributed to increased I-TP, it occurred several years earlier than in the pelagic habitat and anticipated the sudden increase in TP. The I-TP threshold value of the shift was estimated at $< 25$ µg P.L$^{-1}$, a value that was, of course, subjected to the uncertainty in I-TP reconstruction, but that was undoubtedly lower than the threshold that triggered the drastic change in pelagic communities, revealing a higher sensitivity of littoral habitats to nutrient enrichment. The compared temporal dynamics of the littoral and pelagic communities suggested that the macrophyte belts might have also played a role in buffering the response of the lake TP facing increasing loads; at some points, they even benefitted from it, limiting sediment resuspension and phosphorus release and favouring nutrient retention (van Donk *et al.*, 1993; Scheffer & Jeppesen, 1998; Hilt, 2015) until a nutrient threshold was met. Therefore, the sudden loss of the macrophyte stabilizing nutrient effect fostered a direct response of lake nutrient concentrations to loadings from the watershed within the following years (Genkai-Kato & Carpenter, 2005), leading to fast and hasty hyper-eutrophication. Because this transition also occurred during a transient warmer period, potential changes in lake water levels or runoff could have contributed to the sudden reduction in macrophyte coverage, although experimental and observational results indicated submerged macrophyte resilience to warming (Mckee *et al.*, 2002; Kosten *et al.*, 2011), even in situations of synchronous nutrient enrichment. Despite the baby-boom high birth rates, the demography during the 1940s follows the same increasing trend than the one in the previous decades i.e. on average +588 inhabitants.yr$^{-1}$ during the 1931-1936 period and +552 inhabitants.yr$^{-1}$ between the 1936-1951 period (Chapter 2, Figure 2.19). Then, under the assumption that P loadings to the lake scale to the population in the watershed through domestic sewage, nutrient inputs to the scale shall not have suddenly peaked in the 1940s. Thereby, the sudden loss in macrophytic belts would have been triggered by a gradual change in nutrient inputs to the lake, a dynamic expected for a regime shift. Yet, the changes in the nutrient loads to lake have not been documented for this time-period. The indirect evidences we rely on cannot fully decipher whether the sudden loss of macrophytes in the 1940s indeed pinpoints a regime shift or instead an abrupt ecological transition mirroring a sudden environmental upheaval. Nevertheless, the littoral of Lake Varese seemed to have buffered the increasing nutrient loads of the first half of the 20th century arising the increased human activity on its watershed, until macrophyte disappearance.

Littoral species were rare during the hyper-eutrophication phase, and even though their contribution to the total assemblage increased in the most recent period, those are essentially ubiquitous or sediment-associated species (*Monospilus dispar* and *Leydigia acanthocercoides*, *Alona* sp.), rather than those representing the restoration of vegetated littoral areas (*Alonella nana*, *Alonella excisa*, and *Camptocercus rectirostris)* (Bjerring *et al.*, 2009). As a matter of fact, most recent assemblages fall within a density distribution of those observed right after hyper-eutrophication (Figure 4.5 b). The lake phosphorous concentration has significantly decreased but is no longer responding to further reductions in nutrient loads, suggesting a hysteretic response of I-TP itself (Genkai-Kato & Carpenter, 2005). Because the initial critical transition occurred at low I-TP values, which is far below the current one, we had no opportunity to fully test for bistability. Nevertheless, the re-oligotrophication trajectory of littoral habitats has not occurred along the reciprocal pathway; this time, this phenomenon cannot be attributed to climate warming. Bearing in mind that EWS are not diagnostic tools for regime shifts, since they sometimes fail to predict non-linear changes (Burthe *et al.*, 2015), and that regime shifts may also occur without any early warnings (Hastings & Wysham, 2010), the dynamics of EWS are consistent with a loss of resilience. Overall, the transition observed on DCA2 met several requirements to qualify as nutrient-induced shift from one stable state to another, even though the lack of direct data for nutrient loads during this time-period precludes any definitive conclusion. As hypothesized, a critical transition was crossed early in the lake history, at a nutrient threshold that would be difficult to reverse. Transient outbreaks in *Eubosmina* sp. in the late 19th and early 20th century (1856, 1874 and 1918) could even be interpreted as an early flickering process; i.e., the system started jumping back and forth between the different basins of attraction, which is more likely than a critical slowing down under these circumstances (Wang *et al.*, 2012). Although the shift in the littoral area followed the theory of a shallow lakes regime shift, the absence of recovery may now be tied to internal P loadings creating a new positive feedback loop.

## 4.6 | CONCLUSION

Our analysis revealed that continuous and abrupt responses to environmental drivers can occur within a single lake and that critical transitions can be habitat dependent. The increasing nutrient load in the early 20th century in Lake Varese triggered spatially and timely segregated ecological responses acting in destabilizing chain reactions. Because large and deep lakes are spatially heterogeneous, and their pelagic-benthic habitats are less connected than in shallow lakes (Vander Zanden & Vadeboncoeur, 2002; Tunney *et al.*, 2012), the littoral habitats can endure alternative stable states that are desynchronized, in timing and dynamics, with the pelagic areas (van Nes & Scheffer, 2005). Our results suggest that monitoring littoral areas could indicate the signals of abrupt changes, even in deep lakes, as a littoral shift is preceded by a recorded loss of resilience. Today, the nutrient-rich, pelagic ecosystem is highly sensitive to climate warming. This means that in the case of Lake Varese, the combination of new factors are counteracting restoration efforts, further reducing the ecosystem potential for returning to its pre-disturbance functional state as it is driven further from its safe operating space (Scheffer *et al.*, 2015).

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# Chapter | 5

# Lakes vulnerability to climate change in the Anthropocene

## 5 | LAKES IN THE ANTHROPOCENE ARE MORE VULNERABLE TO CLIMATE VARIABILITY

**Rosalie Bruel (1), Stéphanie Girardclos (2, 3), Aldo Marchetto (4), Katrina Kremer (2, 5), Christian Crouzet (6), Jean-Louis Reyss (7), Pierre Sabatier (7), Marie-Elodie Perga (1, 8)**

*Submitted*

(1) CARRTEL, INRA, Université Savoie-Mont Blanc, 74200 Thonon-les-Bains, France

(2) Dept of Earth Sciences, University of Geneva, Rue des Maraîchers 13, CH-1205 Geneva, Switzerland

(3) Institut des Sciences de l'Environnement (ISE), University of Geneva, Boulevard Carl Vogt 66, CH-1205 Geneva, Switzerland

(4) CNR-ISE, 28922 Verbania Pallanza, Italy

(5) present address: Swiss Seismological Service, ETH Zurich, Sonneggstrasse 5, 8092 Zurich, Switzerland

(6) ISTerre, Université Savoie-Mont Blanc, CNRS, IRD, IFFSTAR, UGA 73370, Chambéry, France

(7) EDYTEM, Université Savoie-Mont Blanc, CNRS, 73370, Le Bourget du Lac, France

(8) IDYST, Université de Lausanne, Mouline, 1015 Lausanne, Switzerland

Authors contribution: *RB, SG, MEP conceived the study and interpreted the results. RB, SG, KK, PS, CC, JLR conceived the age model. AM and RB analyzed the core sub-fossil samples. All authors contributed to the writing.*

## 5.1 | ABSTRACT

Alleviating local human forcings is expected to limit ecosystems vulnerability to climate change, although the formal test of this assumption is limited by the lack of long-term data. Relying on an accurately dated composite sediment core, we show that the ecological status of Lake Geneva, the largest lake in Western Europe, has resisted to climate variability for 1,200 years, despite thermal amplitudes similar to those observed during the 20th and 21st centuries. The ecological upheaval of the 1950s, due to local human impact have made this aquatic system more vulnerable to climate fluctuations, despite the management practices implemented in the 1970s. In a world where all ecosystems are exposed to climate change, the urge to preserve them from local human impact, which appears as a major vulnerabilizing factor, is compelling.

*Keywords | Resistance, resilience, climate warming, non-stationarity, non-linearity, temporal ecology, palaeo-ecology, lake, Anthropocene.*

## 5.2 | INTRODUCTION

Anthropogenic climate change impacts most ecological processes worldwide (Scheffers *et al.*, 2016). As ecosystems are being pushed near their limits, there is a popular view that alleviating local human forcings will foster ecosystems resilience to climate change (Scheffer *et al.*, 2015; Rocha *et al.*, 2015). Building ecosystems resilience, i.e the ability of a system to withstand external stresses and disturbances (Gallopín, 2006), is in fact one of the major guideline stated by the UNEP roadmap to maintain ecosystems functions and services (Epple & Dunning, 2014). Resilience is expressed either by the capacity of a system to resist change when facing a disturbance (resistance) or to return to a stable state following disturbance (recovery) (Hodgson *et al.*, 2015).

Empirical studies support the assertion that adequate management of ecosystem diversity could increase ecosystems recovery in cases of discrete extreme forcing such as forest fires (Virah-Sawmy *et al.*, 2009), coral bleaching events (Côté & Darling, 2010; Nash *et al.*, 2016), and droughts (Van Ruijven & Berendse, 2010), but also their resistance (Tilman, Reich & Knops, 2006; Grime *et al.*, 2008; Isbell *et al.*, 2015). Indeed, a more diverse community (horizontal diversity) is more likely to host a larger panel of responses to environmental change, thereby increasing the probability of persistence and recovery after a disturbance. Recovery is more likely in ecosystems that includes cross-scale redundancy, i.e. member of a same functional group operating at different space scales (Nash *et al.*, 2016). Furthermore, the patchy distribution of species in heterogeneous habitats would desynchronize climatic-driven fluctuations in populations (Holling, 1973; Loreau *et al.*, 2003). In addition, a reduction in horizontal diversity can trigger an extinction cascade (Srivastava & Bell, 2009). Yet, these quantitative assessment of resilience have been carried out for stationary environmental variable, i.e. stochastic perturbations, with fixed, underlying probability distributions (Wolkovich *et al.*, 2014). Promotion of resilience (recovery being the most likely aspect) would buffer the consequences of stationary components of climate change.

However, atmospheric warming, the main component of climate change, is a highly non-stationary phenomenon. In this context, resistance, rather than recovery, seems a more desirable property. Fewer attempts to quantify the ecological resilience of a system to persistent abiotic factors can be found, maybe because resistance implies long-term studies. This gap has the potential to question fundamental assumptions of many ecological concepts, models and approaches, as current models may not apply under a new set of stressors (Wolkovich *et al.*, 2014; Schindler & Hilborn, 2015). Resistance to slow-moving persistent forcings relies on internal feedbacks (Foley *et al.*, 2003; Henneron *et al.*, 2015). For instance, forest and peatlands can regulate their own microclimate and soil conditions. Yet, there is a fragile trade off between an optimal resistance and a functional diversity that can still guarantee ecosystem functioning and stability (Henneron *et al.*, 2015).

If biodiversity, habitat patchiness, and high functional diversity are keys factors for resilience to extreme events, similar mechanisms could maximize resilience toward non-stationary environmental variable (see Virah-Sawmy *et al.*, 2009 for instance). Yet, local human impacts are known to be major disrupters of both biodiversity and habitat heterogeneity (Bajard *et al.*, 2017). We posit here that the increasing local pressure on ecosystems impaired their resistance to climate variability. Defining vulnerability as the opposite of resistance, and thereby by the degree of changes in an ecosystem state that can be attributed to a given disturbance, our objective was to assess whether vulnerability of ecosystems to climate variability has been altered due to past or present local human impacts.

In Central Europe, over the period of 800-1800 AD alone, summer air temperature (SAT) anomalies fluctuated within a range of 3°C (Büntgen *et al.*, 2006)(Büntgen *et al.*, 2006), which fall into the same amplitude as the variations observed over the 20th and 21st centuries. If this period extends beyond the instrumental monitoring records, palaeo-ecology offers the possibility to cover long period of times on a single system, allowing to get rid of the variations linked to geographical area and different local settings. We quantified climate-driven ecological changes over the last 1,250 years (i.e. 755-2010 AD) in a lake with a known and well-documented history of local human impacts, Lake Geneva (France, Switzerland). We aimed at testing whether similar thermal amplitudes generated more important climate-driven ecological changes once the lake had been impacted by anthropogenic activities. For that purpose, biological proxies (diatoms and cladocerans) were retrieved and analyzed from an accurately dated composite sediment core. The main challenge lied in distinguishing between the modifications in the planktonic assemblage of Lake Geneva attributed solely to climate variability and those due to local human impacts; and then to compare the magnitude of climate-driven changes under different regimes of local human impact (low vs. high). Ordination methods and change point analysis were thereby used to describe the main dynamics within the assemblage while general additive models (GAM) quantified the drivers of successive ecological changes.

## 5.3 | MATERIALS AND METHODS

### 5.3.1 | STUDY SITE

Lake Geneva is the largest lake of Western Europe, with a maximum depth of 309 meters. The human population in its watershed has increased threefold since the late 19th century, directly initiating the well documented eutrophication. Maximum Total Phosphorus (TP) concentrations reached 90 µg $P.l^{-1}$ in the late 1970s. Management practices successfully controlled the lake phosphorus concentrations as early as the 1980s (Anneville & Pelletier, 2000). Observed concentration in Lake Geneva has been below 20 µg $P.l^{-1}$ since the 2010s. Although Lake Geneva's hydrological function had been impacted since the first dam was built in the late 19th century at the lake outflow, it is the changes in TP that have triggered the onset of deep water hypoxia (Jenny *et al.*, 2014) as well as quantitative and qualitative changes in planktonic (Anneville & Pelletier, 2000; Alric *et al.*, 2013; Berthon *et al.*, 2014) and fish (Anneville *et al.*, 2017) populations since the 1950s. At the same time, the regional atmospheric warming has reached +2°C over the 20th century, i.e., twice the global average, with a first warming phase starting in the 1930s and 1940s. Evidence suggests that the most recent atmospheric warming (since the 1980s), superimposed on fluctuations in TP, has altered the physical, biogeochemical, and ecological structure of Lake Geneva (Alric *et al.*, 2013; Perga *et al.*, 2015; Anneville *et al.*, 2017).

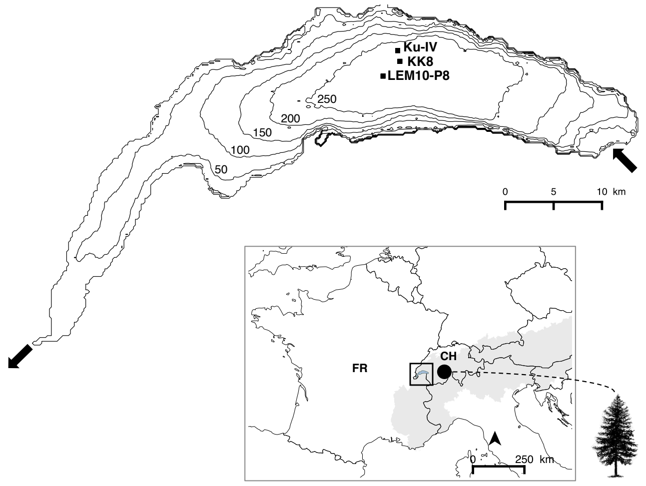

**Figure 5.1 |** Map of Lake Geneva location.

Lake Geneva lies at the border between France (FR) and Switzerland (CH) in the peri-alpine domain (Alps as grey surface on the bottom-right insert map). The bathymetry (in meters) and sediment core localization (black squares) are indicated. Arrows indicate the Rhône river inflow and outflow. The black circle on the bottom insert map shows the location of the four trees-ring sites used by Büntgen *et al.* (2006) to reconstruct SAT anomalies.

### 5.3.2 | SEDIMENT RECORD AND DATING

A palaeo-record dataset was built using three sediment cores collected in 2010 in the deepest basin of Lake Geneva (Figure 5.1). The main sediment archive is a long core covering the past 4,000 years (Ku-IV, 12 m, Long. E 6.60810/ Lat. N 46.47652, sampled on 02/09/2010) published by Kremer *et al.* (2012, 2015c). From this previously dated and studied core, only the 4.31 upper meters of the sediment sequence situated above the Tauredunum deposit of 563 AD documented by Kremer *et al.* (2012) were analyzed. As the top of Ku-IV was neither complete nor well preserved, the last ~100 years of the record could not be considered for this core. Thus, we used two short surface sediment cores as complementary archives to fill this gap. One first short core, very similar to Ku-IV and located only 1.1 km southward, was used to solve the chronology issue of the past ca.100 years (KK8, 1.31 m, Long. E 6.61124/ Lat. N 46.46665, sampled on 19/04/2010). To build a coherent chronology two closely spaced sediment records were merged into one composite core LEM10-CC using the stratigraphic level of turbidite t2 (47.5-51.5 cm on KK8, 54.5-61.5 cm on Ku-IV) as identified by Kremer *et al.* (2015a) in both records (Figure 5.2 a). A second short core analyzed by Alric *et al.* (2013) (LEM10-P8, 0.4 m, Long. E 6.58872/ Lat. N 46.45270, sampled in May 2010), collected 3 km away from Ku-IV, served as high resolution complement for cladoceran assemblages. LEM10-CC and LEM10-P8 were merged using the depth dated as 1963 (12 cm on LEM10-CC, 24.1 cm on LEM10-P8, Figure 5.2 b), inferred from a good radionuclide dating as well as a clear change in the cladoceran assemblage. The overlap between the three cores corresponds to the time interval between the Little Ice Age (LIA) and the mid 20th century, i.e. a period of marked climatic transition and increase of human activities in Lake Geneva's watershed. It was thus crucial to obtain robust data for this overlapping sediment interval, to ensure that the transition from one record to another was not introducing a methodological bias.

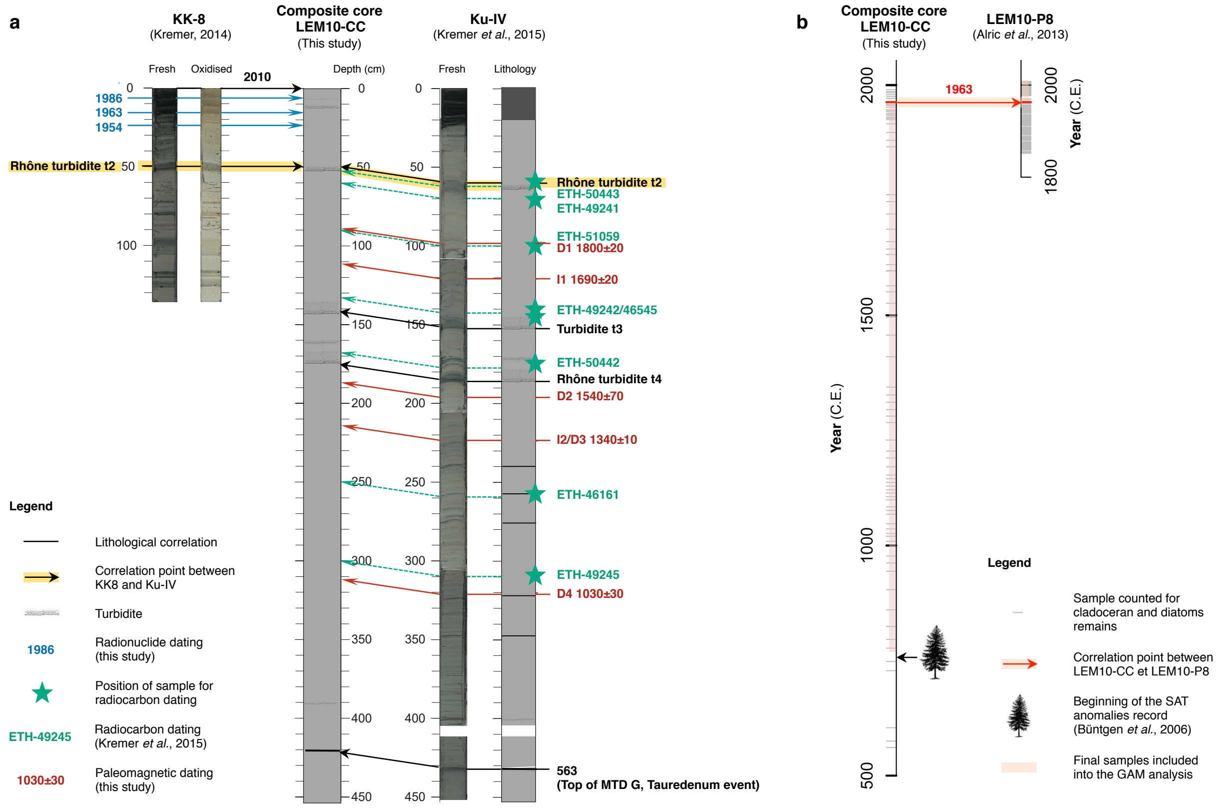

**Figure 5.2 I** Construction of the composite core.

(a) Construction of the composite LEM10-CC sediment record with core photographs and lithology description used in this study. From left to right, KK-8 (fresh sediment), KK8 (oxidized sediment), LEM10-CC composite core (lithology), Ku-IV (fresh sediment), Ku-IV (lithology). The lithological correlations are represented with black lines and arrows. Dated horizons are represented by blue ($^{137}$Cs activity peaks), red (palaeomagnetism) and green (radiocarbon) lines and arrows, and stars, respectively (see legend); the corresponding ages are written next to the horizons. (b) Construction of the composite cladoceran records between LEM10-CC and the high-resolution LEM10-P8 (Alric *et al.*, 2013) from the well dated 1963 horizons.

The chronology of the composite core LEM10-CC was already constrained on the 563-2010 time-period by the Tauredunum deposit event and the coring year. The new chronology add data from short-lived radionuclide activities and palaeomagnetic secular variations allowing a rare dating precision in regards to the length of the core. From the event free composite core LEM10-CC, we calculated a continuous age-depth relationship with the R-code package 'Clam' version 2.2 (Blaauw, 2010b) and compared the output with the Bayesian model Bacon (Blaauw & Christen, 2011). All details are provided in Chapter 2.

### 5.3.3 | SELECTION OF CLIMATE DATA

A substantial climatic variability has been reported for the past 1,500 years in central Europe. A notably cold period was likely triggered by a volcanic eruption in the 'Dark Age', 536–660 AD (Larsen *et al.*, 2008; Büntgen *et al.*, 2016), followed by a prolonged period of relative climate stability (Medieval Quiet Period, ~725–1025 AD, Bradley *et al.*, 2016). The ensuing Medieval Warm Period (MWP, ca. 900–1300 AD) showed average summer temperatures similar to those observed between the 1950s and 1970s (0°C SAT anomaly, Ljungqvist, 2010). There then followed a new cold period, the LIA (ca. 1300–1800 AD; -3°C SAT anomaly, Ljungqvist, 2010) before the recent warming (recent Climate Change rCC, 1850-present, Abram *et al.*, 2016), mainly attributed to human impact.

Climate fluctuations over the past millennia are marked by significant regional offsets (Crowley & Lowery, 2000; Mann & Jones, 2003). It was thus essential to choose a relevant reconstruction of the climatic forcing, but also to understand the region it accounts for, as some signals are more regional than others. We selected a local reconstruction of SAT anomalies from the Rhône valley, directly linked to Lake Geneva (Büntgen *et al.*, 2006). The record goes back to 755 AD, restricting our analysis to the last 1,250 years. When cladoceran sample covered several years, an average SAT anomaly was calculated for this period and used in the model.

### 5.3.4 | RECONSTRUCTION OF TP LEVELS

In Lake Geneva, a long-term monitoring program, initiated in 1958, spans the majority of the eutrophication and the re-oligotrophication phases. Changes in total phosphorus concentrations (Berthon *et al.*, 2013) were inferred from diatom sub-fossil remains for the previous period when there was no monitoring data (see Chapter 2). Changes in diatom inferred-TP are considered as representative and indicative of the local human activities in the lake watershed (Battarbee *et al.*, 2005). The composite TP record is thereafter referred to as I-TP.

### 5.3.5 | ECOLOGICAL DYNAMIC

Cladocera were regarded as the main proxy for ecosystem state, as they show high sensitivity to changes in the environment, recording bottom-up changes in resources, alterations in habitat structure, and diversity and top-down impacts of predation (Davidson *et al.*, 2011).

Continuous sub-sampling of LEM10-CC was carried out, and one out of three samples were selected for Cladocera remains counting. The time-periods before and after anthropogenic influence are likely to lead to different degrees of depositional impact (a millennium of lower local human impact is to be compared to the past century of high local human impact). Thereby, the sampling interval needed to be adapted and tightened in the recent period to avoid any statistical false positives that would result from a low number of data points. The sampling interval was also tightened for the MWP to ensure the different time-resolution would not impact the results. After a careful check on the coherency between studied records, the recent high resolution cladoceran data from Alric *et al.* (2013) was used within our sediment record.

The cladoceran remains were analyzed for LEM10-CC according to Frey (1986) with the same method as Alric *et al.* (2013) for LEM10-P8. A minimum number of 400 cladoceran remains per sample (headshields, shells, post-abdomens, post-abdominal claws, mandibles and others) were counted and identified using the determination keys of Szeroczynska and Sarmaja-Korjonen (2007) and an Olympus BX41 microscope at 100-200 magnification. *Bosmina* sp. were determined to the species level (*B. longirostris*, *E. longispina*, and *E. coregoni*), as well as chydorids, whenever possible. Regarding the complexity of the taxa (Alric *et al.*, 2016), *Daphnia* spp. were identified to the genus level.

### 5.3.6 | STATISTICAL ANALYSIS

The main dynamics of the cladoceran community over time were summarized using Principal Component Analysis (PCA), after Hellinger transformation of the percent data, and significant changes in the mean of the PCA scores were detected using Changepoint analysis (Killick *et al.*, 2016). The significance of each change point was tested comparing the number of detected change points as compared to those that can be on average expected for a random series, using the Pruned Exact Linear Time method constrained by a penalty. The penalty was determined by the incremented Akaike information criterion (AIC) method and verified manually by drawing an elbow plot.

The relative contribution of changes in I-TP (Chapters 2-3) and climate (SAT anomalies) to the dynamics of PCA scores were assessed by using the Generalized Additive Models (GAMs, Wood, 2016). The final GAMs were chosen by computing models using I-TP and SAT as covariates, and the best models were chosen following the AIC. Then, the choice to include or not a correlation structure (AR (1) or CAR (1) to account for uneven sampling) was made using the log-likelihood of each model. The competing forcing variables and their effects were separated based on the computed contribution of each covariate to the fitted model (Simpson & Anderson, 2009).

The first ordination axis summarized the changes driven by eutrophication, and allowed to set the moment when Lake Geneva ecological responses started to be driven by local human impact i.e. in between 1946 and 1952. The initial hypothesis is that a change in vulnerability took place since Lake Geneva early eutrophication, and despite its restoration. GAM was thereafter applied separately on the second ordination axis scores for the two time-periods ('pristine' 777–1946, 1952–2010 'impacted'). The two datasets contained 63 and 38 datapoints, respectively. A sensitivity analysis was conducted in order to evaluate if the results depended on the date considered as the limit between the pristine status and an impacted system, repeating the analysis for all possible dates ranging from 1114 to 1987. In this way, 20 points at least were left for fitting a model in every analysis. We then performed GAM with SAT anomalies as the main covariate for the different subsets. For each run, we tested whether or not a correlation structure for the model errors was supported by a likelihood ratio test.

## 5.4 | RESULTS

The age model for LEM10-CC integrates 11 stratigraphic horizons: i) the coring year, ii) three time markers from $^{137}$Cs profile, iii) the age of turbidite t2 from $^{210}$Pb$_{ex}$ activities, iv) five dated points from the new palaeomagnetic study, together with v) the 563 AD historical time marker. The best Clam model was obtained using a smooth spline interpolation (smooth= 0.32), which avoids sudden change in sedimentation rates (Figure 5.3). The independent Bacon model run for comparison displayed the same trend (Chapter 2). The Clam model was favored because it better fits the original time markers of radionuclides activities that are important for a precise 20th century chronology.

The LEM10-CC age model reveals younger ages than previously estimated (Kremer *et al.*, 2015a). $^{14}$C dates are typically older due to the classical effect of terrestrial organic macroremain reworking in the catchment. On the other hand, palaeomagnetic chronology may be affected by the lock-in depth (i.e. the delay in acquisition of the primary magnetization), that implies that sediments are systematically older than the geomagnetic feature they preserve (Sagnotti *et al.*, 2005; Mellström *et al.*, 2015). We chose the palaeomagnetism dating over the $^{14}$C dates because their uncertainties ranges at the centimeter scale (Katari *et al.*, 2000), i.e. decadal scale in Lake Geneva, instead of century scale errors in the case of $^{14}$C. Besides, this palaeo-magnetism based model intercepts the age error of the four $^{14}$C retained by Kremer *et al.* (2012), confirming their realism (Figure 5.3).

Merging of the new cladoceran counts on the long record LEM10-CC with the high-resolution data of LEM10-P8 (Alric *et al.*, 2013) was accepted only because the general Lake Geneva species dynamics could really well be matched from one core to the other (*Daphnia* spp. went up from representing 50% to 90% in both cores; Chapter 2). Because we have a high confidence in the dating for this period, thanks to radionuclides dating performed by the same method in the two short cores (Alric *et al.*, 2013), we created the composite core at this date i.e. LEM10-CC until 1961 and LEM10-P8 from 1963 ( b). As Alric *et al.* (2013) identified Chydoridae at the family level, we grouped all the remains belonging to this family together to be consistent among the two records. As no particular change in the cladoceran assemblage could be found among the Chydoridae species, representing always less than 5% of the total assemblage at any given stratigraphic level, we have good confidence that key information within the other groups was well preserved. More details regarding the chronology and the creation of the composite core are given in Chapter 2.

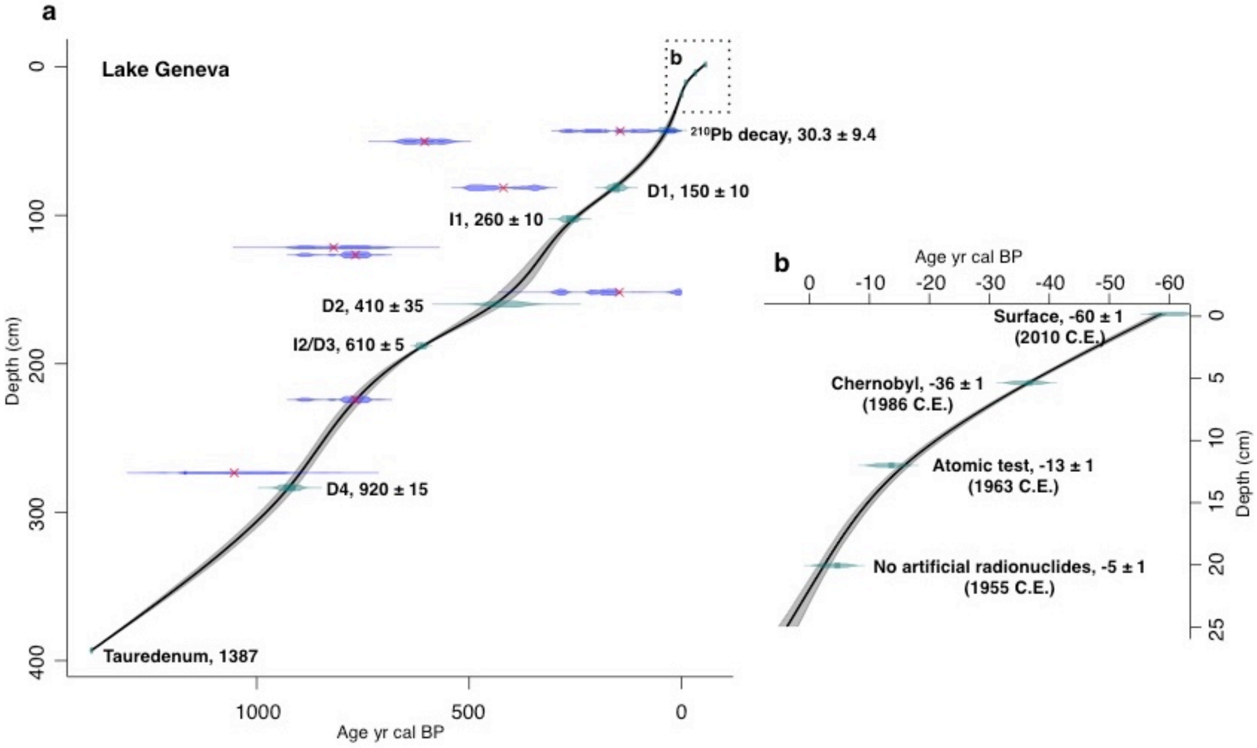

**Figure 5.3 I** Age-depth model of composite core LEM10-CC built with Clam R-code package (Blaauw, 2010a) from 11 stratigraphic horizons.

(a) Total record and (b) zoom on the three $^{137}$Cs dates. Event layers with thickness above 1 cm were interpreted as instantaneous events (Kremer *et al.*, 2015a) and removed before the age model computation. The envelope (grey area) represents the 2-sigma probability interval. Data not used to fit the age model are marked with a red cross. See Chapter 2 for details.

TP concentrations inferred from diatom assemblages confirm that no significant changes in I-TP were recorded for the period 563–1957 AD (Figure 5.4 c&d) despite a long history of human occupation in Alpine Europe (Kaplan, Krumhardt & Zimmermann, 2009). Major ecological changes were summarized by two primary principal components of the cladoceran assemblages (PC1 and PC2, Chapter 3) of the ordination analysis that accounted for 90% of the total variability within the dataset. Over the past 1,450 years, only three changes were detected in the assemblage and all three occurred in the past 80 years. Moreover, our results show that the 'recent' cladoceran assemblage is radically different from the one characteristic of the 563–1940 period, underlying the relevance of palaeolimnological tools even for lakes that have been surveyed as early as the late 1950s such as Lake Geneva.

From the beginning of the record and for twelve centuries, the cladoceran community of Lake Geneva was dominated by the same two species, the pelagic *Eubosmina longispina*, the earliest postglacial colonist in alpine lakes (Nauwerck, 1991), and *Sida crystallina* var. *limnetica* (Figure 5.4 e&f). The latter species occupies both pelagic and littoral habitats (Forel, 1892), which support the likely presence of macrophytic belts around the lake before the 20th century. The most important transition in the community composition in 1946–1952 is explained by PC1 and was manifest as the increased absolute abundance of both *Daphnia* spp. and *S. crystallina*. Ten years later, *Daphnia* spp. eliminated *E. longispina,* while the habitat-demanding *S. crystallina*, that had been continuously present since 563 AD, almost vanished in Lake Geneva in 1963. Such successive transitions have been confidently attributed to eutrophication (Chapter 3), and occurred at a relatively low I-TP threshold of 10–20 $\mu gP.L^{-1}$. Between 1946 and 1963, the pristine Lake Geneva, hosting both littoral and planktonic habitats, shifted to an anthropogenic impacted, plankton-dominated state. We thereby use this 1946–1963 transition as marking point for the beginning of the Anthropocene regarding the lake's ecosystem. While this period correspond to the latest consensus on the formal onset of the Anthropocene, following World War II (Zalasiewicz *et al.*, 2017), we acknowledge the very local source of perturbation in the case of this study.

Because nutrient-driven ecological changes are well depicted by PC1, the ecological modifications, accounted for by the orthogonal PC2, are independent of eutrophication. The second ordination axis is important to consider despite a low percentage of variation (7%) because the identified transitions are consistent with significant changes in assemblage observed at the community level (Chapter 2-3). Two transitions are identified on the second ordination axis, in the periods 1934–1937 and 1981–1982. The 1934–1937 transition occurred in the littoral habitat, with a transient increase in the abundance of *S. crystallina* (making up to 40% of the assemblage), until the nutrient-driven loss of their habitat in 1962. In contrast, changes in the assemblage since 1982 have been observed in the pelagic habitat, with the diversification of *Eubosmina* species (*E. longispina* and *E. coregoni*) and the unprecedented presence of *Leptodora kindtii*.

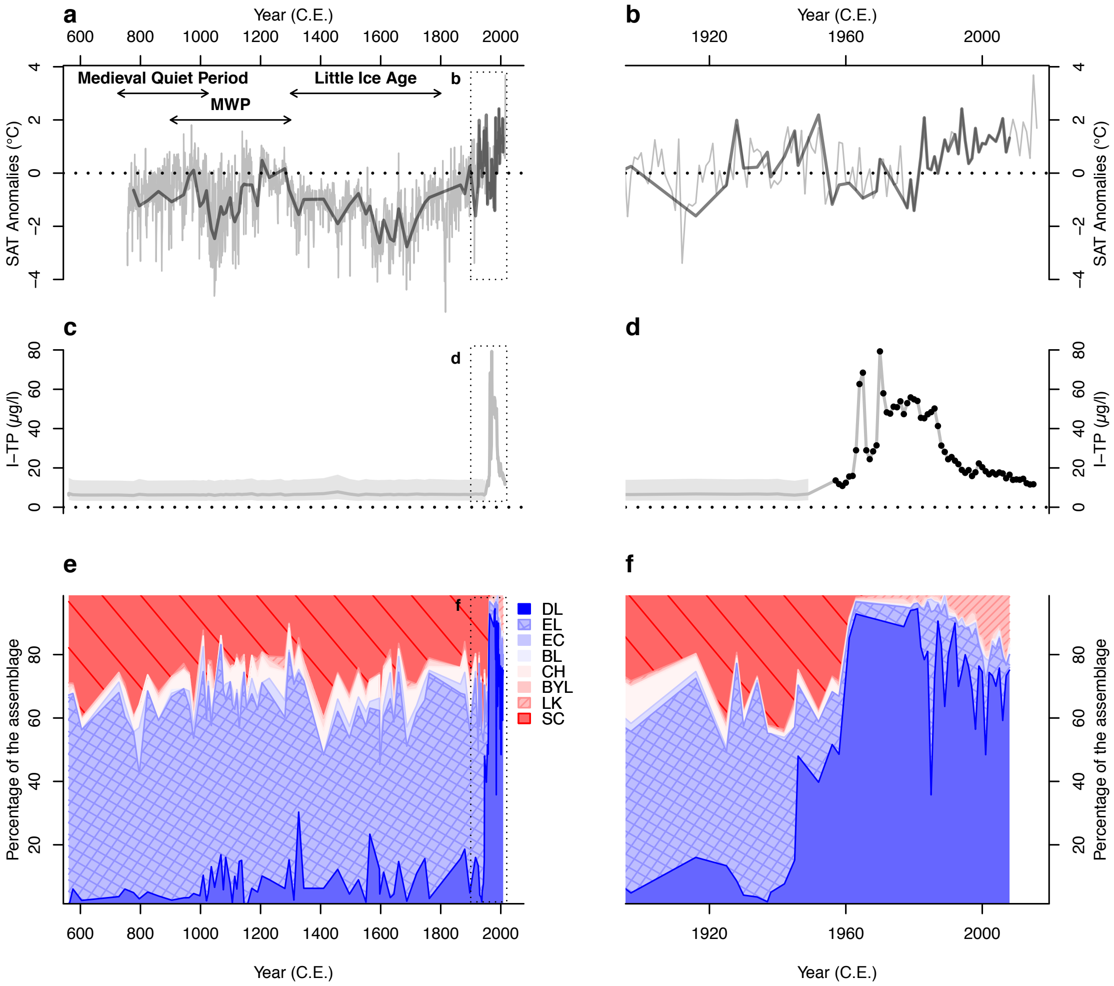

**Figure 5.4 I** Changes in temperature, phosphorus, and cladocera assemblage since 600 AD.

(a, b) Reconstructed summer (June to August) air temperature anomaly (SAT anomaly) from the Rhone valley (Switzerland) for the 755–1960 time period . Measured SAT converted into SAT anomaly at the Cointrin weather station (Switzerland) for the 1961–2016 (a) **and 1900–2016** (b) **time-interval**. Light grey line represents annual data; dark grey line represents the selected temperature for each sample, accounting for changes in sample thickness and sedimentation rate. (c, d) Diatom-inferred total phosphorus (DI-TP) (thick grey line, with confidence interval) compared to the monitoring data for the 1961–2016 (c) **and 1900–2016** (d) **time-interval** (SOERE SI-OLA, Thonon-les-bains, France). (e, f) Changes in cladoceran assemblage for the 1961–2016 (e) **and 1900–2016** (f) **time-interval**. DL: *Daphnia spp.*, EL: *Eubosmina longispina*, EC: *Eubosmina coregoni*, BL: *Bosmina longirostris*, CH: Chydoridae sp., BYL: *Bythotrephes longismanus*, LK: *Leptodora kindtii*, SC: *Sida crystallina*.

The contribution of climate variability to the ecological modifications explained by PC2 (ecological changes independent from local human impact, depicted by PC1) was extracted from specific model runs for the periods before 1946 and after 1952. For each period, GAMs could identify the amount of ecological variance (PC2) that could be explained by climate variability. If climate explains a high percentage of the ecological variability, the vulnerability to climate is considered high. Vulnerability to climate variability is depicted by a null relationship prior to 1946 (Figure 5.5 a), attesting that prior to the mid-20th century, the substantial climate variability (3°C amplitude, Figure 5.4 a) did not associate with any significant changes on cladoceran assemblages. In contrast, the significant relationship favoring negative scores, i.e., the pelagic predator *Leptodora kindtii* and *Eubosmina* sp. for post-1952, highlights the contribution of recent warming to the current cladoceran assemblage (Figure 5.5 b). The direct (through water temperature) and indirect pathways (through fish predation pressure), by which recent climate warming (after 1980) have been shaping Lake Geneva pelagic food web, have been documented in Alric *et al.* (2013). Picking any date between 1730 and 1978 as the limit for the anthropogenic-impacted state reaches similar conclusions (Figure 5.5 c). Thereby, eutrophication in Lake Geneva not only drove the major rearrangement in the cladoceran assemblage over the course of the past 1,250 years but also increased the vulnerability of this zooplankton compartment to climate variability.

## 5.5 | DISCUSSION

We show that from 563 AD until the beginning of the 20th century, ecological state of Lake Geneva as depicted by cladoceran assemblages remained stable despite the climate variability evidenced by local reconstructions (Büntgen *et al.*, 2006). TP levels remained low indicating a good buffering capacity of the system in regards to the land occupation in the Alpine area over this period (Kaplan *et al.*, 2009). The sediment archive mirrored the well-documented eutrophication phase in Lake Geneva, that started at low levels of TP (< 10 µg P.l$^{-1}$), and led to the dominance of pelagic taxa. Despite recent ecological responses to decreasing TP are measured, more climate-induced changes could be observed in past 70 years than for the previous millennium. We interpret this as an increased ecological vulnerability of Lake Geneva to climate variability i.e. a loss of resilience.

The explanation for this change in vulnerability must consider whether humans have locally altered the lake thermal behavior. Because of direct (lake level regulation) or indirect human impact (hydropower systems and regulations in the Rhone River, which supplies 70% of the lake water), the sensitivity of lake water temperature to atmospheric warming might have been exacerbated in the last century. The absence of any ecological response to the known atmospheric warming during the MWP might be due to a former relative disconnection between air and lake water temperatures. Yet, the coherent response of lake surface water temperature in very dissimilar lakes in different geographical regions suggests that large-scale atmospheric forcing on synoptic timescales is the major driver of lake surface temperatures despite their hydrological differences (Livingstone & Padisák, 2007; Livingstone *et al.*, 2010). Furthermore, the surface temperatures of deep lakes, such as Lake Geneva, have been shown to be particularly sensitive to atmospheric warming due to their high thermal inertia (Woolway & Merchant, 2017) and this sensitivity is amplified in deep peri-alpine lakes in summer (Pareeth *et al.*, 2017). Overall, the heat budget of large lakes is relatively insensitive to their tributaries while almost exclusively depending on atmospheric parameters (Fink *et al.*, 2014). It is, thus, unlikely that the lake water temperature did not change with climate over the 1,200 years preceding the Anthropocene.

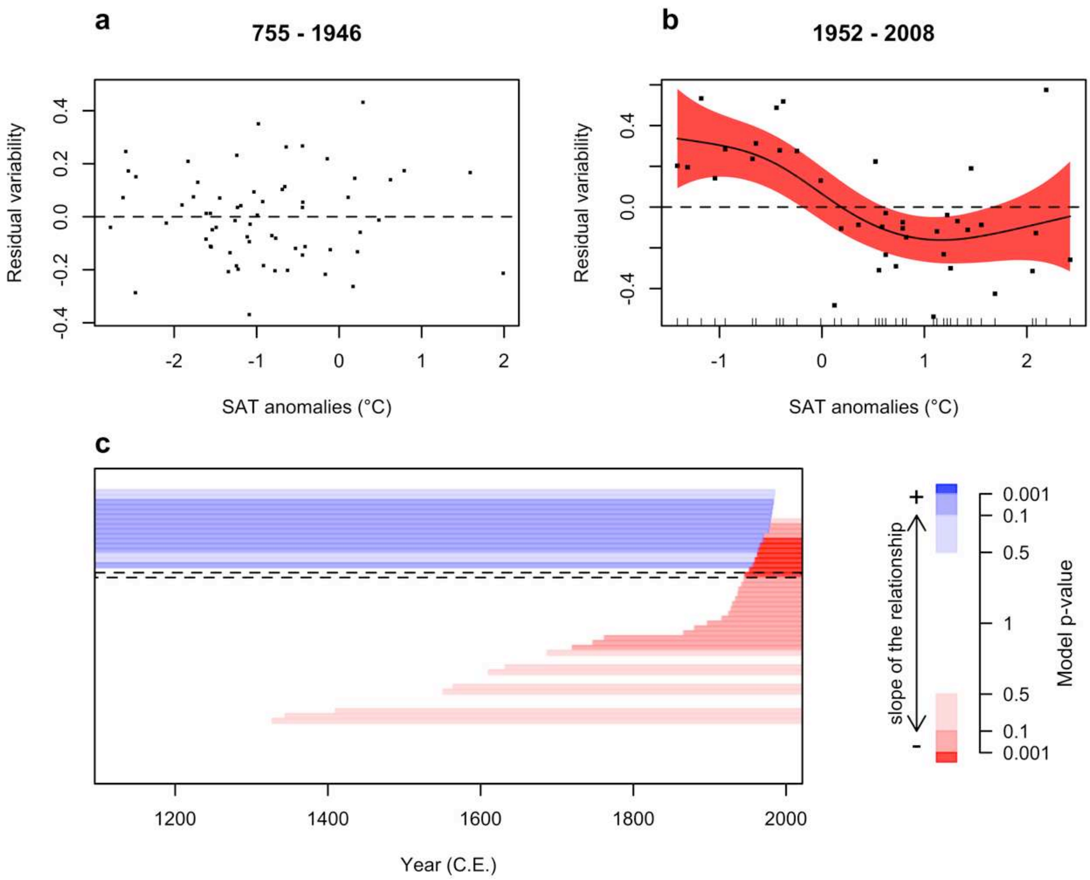

**Figure 5.5 I** Ecological vulnerability of Lake Geneva to climate variability under two regimes of local human impact.

The line depicts the fitted model between those two components and the shaded area at the 95% confidence interval. Each tick mark inside the x-axis corresponds to one observation used to fit the model. (a, b) Relationship between the residual variability in the cladoceran assemblage (PC2, i.e. the variability not driven by I-TP) and SAT anomalies for (a) the 777–1946 C.E. period and (b) the 1952–2008 C.E. period. (c) Test of windows. The x-axis set the limit date at which the datasets were split. The different colours reflect the significance of the model fitted to SAT anomalies as well as the slope of the relationship in order to depict the change in the regime of vulnerability for the time period before and after the limit date. More examples of fitted relationship for different splitting date are presented in Chapter 3.

Another explanation does not involve the relative magnitude of SAT changes (within 3°C between both time periods) but their absolute values. Since the 1940s, SAT values have exceeded the maxima of the previous 1,250 years. The lake ecology could be more sensitive now than before the 20th century because a threshold in atmospheric temperatures has been crossed. Concerning lake hydrodynamics, this temperature threshold would be materialized by the shifts in lake mixing regimes, i.e., atmospheric warming could cause a shift from a dimictic to a monomictic regime, with subsequent changes in lake ecology, as observed in Arctic and sub-arctic lakes (Arp *et al.*, 2016). Since its surface doesn't freeze in winter, Lake Geneva is currently monomictic and it is very unlikely that it has been dimictic at any time during the last millennium, even during the coldest periods (Forel, 1892) of the LIA. In fact, since ice cover can easily be observed and draws the attention of local population, the 'lake icing' intervals are usually recorded in local chronicles (Garnier, 2016). Lake Geneva has been ice-covered and only in the small external basin, only 14 times during the LIA (Forel, 1892; Garnier, 2016). Thereby, even though the timing and strength of stratification and mixing might have changed over time, it is unlikely that Lake Geneva has undergone a change in the mixing regime strong enough to generate a thermal threshold that could drive an ecosystem shift.

It seems that before the 1950s, the ecological status of Lake Geneva, as mirrored by cladoceran (and diatoms, see Chapter 2) communities, was not vulnerable to changes of 3°C in air temperature and its consequent effects on lake water temperature. Since the 1950s, climate variability has been an important driver of the ecological status, indicating a higher vulnerability to recent atmospheric warming. It is then reasonable to consider that the ecological vulnerability to climate change is not only tied to the rate at which water is warming but also to inherited local human alterations of the lake food web. This conclusion is supported by a recent diachronic approach conducted at the neighboring, oligotrophic Lake Annecy under the same climatic context, where the lake surface water temperature has increased by 4°C between the 1970s and the 2000s (+2.5°C in Lake Geneva) but the cladoceran assemblage has barely responded to the change (Perga *et al.*, 2015).

Besides the magnitude of the temperature increase, the climate-driven changes are also modulated by human interventions. The warmer climate episode that happened in the 1930–1940s in the region around Lake Geneva (Figure 5.4 b) preceded the ecosystem shift attributed to local human activities. This transiently warm episode was not only of similar thermal amplitude to the atmospheric warming observed since the mid-1980s (+2°C SAT anomalies) but it also occurred at the same rate of change (+0.4°C per decade between the 1930s–1940s and 1970s–1980s). However, the responses to these two warming episodes - before and after the eutrophication - have been completely different. The recent mid-1980s warming favored pelagic species while the 1930–1940s episode had limited consequences on overall cladoceran assemblages, causing transiently higher abundances of the macrophyte-associated *Sida crystallina* (Chapter 2-3).

The depositional record indicates that during the 20th century, Lake Geneva has entered a new regime characterized by a higher rate of modification of the cladoceran assemblage and a change in its vulnerability to climate variability. Overall, anthropogenic impacts triggered fundamental structural rearrangements of the horizontal diversity with substitutions in the lake herbivorous community and a simplification of habitat diversity through the loss of littoral areas. Therefore, littoral areas are functionally crucial components of habitat heterogeneity, biodiversity, and resilience, even in a large and deep lake for which their representability is always minor.

A second look at previously published long-term reconstructions suggests that Lake Geneva is probably not the only large-sized lake for which eutrophication triggered changes in vulnerability to climate. The diatom subfossil remains in Lake Garda (Milan *et al.*, 2015) or DNA archives of eukaryotic communities in Lake Bourget (Capo *et al.*, 2016), two other large peri-alpine lakes, do not show any significant changes during the MWP with respect to the preceding and following centuries. In northeastern Poland, the resilience capacity of the smaller Lake Żabińskie was surpassed as early as the 1600s (Hernández-Almeida *et al.*, 2017). Since the 1600s, ecosystem variability has markedly increased and biological variables (diatoms, chironomids, and chrysophytes) have been unstable similar to the post-eutrophication status of Lake Geneva.

In the face of multiple stressors to be managed, addressing local or regional drivers could build resilience to continued global change (Rockström *et al.*, 2009a; Rocha *et al.*, 2015). Our findings greatly restrict this statement. In here, we show that eutrophication actually acted as a switch from a regime of resistance to a regime of vulnerability toward climate variability. If local drivers have to be reduced to build resilience, it needs to be done before the ecosystem has been pushed beyond its limits. Indeed, once disturbed, Lake Geneva did not regain its resilience to climate variability. We suspect that lakes are not the only ecosystems concerned by this relationship as a recovery debt (i.e. the interim period during the recovery process characterized by biodiversity and functions deficit) could be measured for various aquatic (oceans, rivers) and terrestrial (forests, grasslands) ecosystems (Moreno-Mateos *et al.*, 2017). Once the resilience against a specific forcing is lost (the ecosystem shift), the general vulnerability of the system increases for all potential forcings (Scheffer *et al.*, 2015). Mitigation of the impacts of climate change and any forcing can be achieved by preserving natural ecosystem resilience (Moreno-Mateos *et al.*, 2017). In that respect, the resistance capacity of the system guarantees a higher stability than its recovery capacity (Vallina & Le Quéré, 2011). Preventing ecological shifts appears crucial because restoration efforts undertaken locally after a perturbation do not guarantee a total recovery of ecosystem functions.

## 5.6 | ACKNOWLEDGMENT

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# Chapter | 6

# Quantitative approach to lakes ecological vulnerability to climate change

# 6 | QUANTITATIVE APPROACH TO LAKES ECOLOGICAL VULNERABILITY TO CLIMATE CHANGE

**Rosalie Bruel(1), Aldo Marchetto(2), Pierre Sabatier(3), Manuela Milan(4, 5), Monica Tolotti(5), Liisa Nevalainen(6), Nathalie Dubois(7,8), Marie-Elodie Perga(1,9)**

*In preparation*

(1) CARRTEL, INRA, Université de Savoie-Mont Blanc, 74200 Thonon-les-Bains, France

(2) CNR-ISE, 28922 Verbania Pallanza, Italy

(3) EDYTEM, Université de Savoie-Mont Blanc, CNRS, 73370, Le Bourget du Lac, France

(4) IASMA Research and Innovation Centre, E. Mach Foundation – Istituto Agrario di San Michele all'Adige, Via E. Mach 1, 38010 S.Michele all'Adige, Trento, Italy

(5) current address: Limnologisches Institut, Universität Konstanz, D-78457 Konstanz, Germany

(6) Faculty of Biological and Environmental Sciences, University of Helsinki, 15140 Lahti, Finland

(7) Eawag, Swiss Federal Institute of Aquatic Science and Technology, Switzerland

(8) Geological Institute, Department of Earth Sciences, Swiss Federal Institute of Technology Zurich (ETHZ), Switzerland

(9) current address: Institute of Earth surface dynamics, University of Lausanne, CH-1015, Lausanne, Switzerland

Authors contribution (so far): *RB and MEP designed the study. RB and AM acquired new biological data. PS dated new sediment material. MEP, MM, MT, LN gave access to data previously published. ND provided a core of Lake Zurich. RB and MEP analysed the data. RB wrote the manuscript as it is presented in this chapter.*

## 6.1 | ABSTRACT

Predicting the impacts of climate change on ecosystems constitutes an important challenge for scientists. The ecological responses are often obscure because they depend on many parameters. For instance, change in temperature may be balanced by a change in another variable (e.g. precipitations), which may result in no change within the ecosystem. Finally, the vulnerability of ecosystems to climate variability may have been disrupted along the past century, increasing the difficulty to attribute with certitude the driver for the changes.

Our objective was to quantify lakes vulnerability to climate warming, and to explain potential discrepancy of vulnerability among several systems. We worked on ten peri-alpine lakes with contrasted eutrophication histories in order to limit the variability of exposition to climate warming but maximise the variability of exposition to local human impacts. We reconstructed the ecological trajectory of these lakes for the past century resorting to palaeo-ecological tools. We selected Cladocera to represent the changes in ecological state and diatoms to reconstruct past-levels of phosphorus. Then, we combined statistical tools to extract the quantity of variability due to climate warming.

We found contrasted levels of vulnerability to climate warming across the systems. Half of the variability was well explained by past levels of total phosphorus in the lake. At the peri-alpine scale, large lakes with an important history of eutrophication displayed more response, i.e. were less resistant, to climate warming.

Eutrophication has been and still is the major threats to surface freshwaters. Our results indicate that even after restoration, the lakes with strongest history of nutrient enrichment show the most responses to climate warming.

*Keywords | climate warming, eutrophication, palaeo-ecology, vulnerability, resistance.*

## 6.2 | INTRODUCTION

After long period of ecological stability during at least the past 2,000 years, large, peri-alpine lakes have undergone under several ecological transitions during the past century (e.g. Bruel *et al.*, Under Review; Alric *et al.*, 2013; Milan *et al.*, 2015; Capo *et al.*, 2016). Yet, despite being located in the same region, hence being exposed to a similar climate, ecological trajectories of lakes vary qualitatively and quantitatively (Dokulil *et al.*, 2010; George, 2010; Alric *et al.*, 2013; Berthon *et al.*, 2014). This seriously hampers our capacity to predict their evolution.

Lake physical response to climate change (e.g. water temperature and stratification/mixing dynamics) depends on both climatic signals and their exposure to climate. Exposure include local characteristics such as lake surface area, fetch and depth (O'Reilly *et al.*, 2015). However, the magnitude of the physical response to climate change did not appear as the only driver of ecological vulnerability on three peri-alpine lakes (Annecy, Bourget, Geneva, Perga *et al.*, 2015). For instance Lake Annecy has shown little ecological changes attributed to climate warming while its surface waters have been warming twice as fast as those of the larger lakes Bourget and Geneva. At the scale of the past 1,250 years, Lake Geneva displayed resistance to climate variability until the 20th century (Bruel *et al.*, Under Review). Lake Varese, a smaller system at the south of the Alpine barrier, shifted in the 1940s; its pelagic assemblage is now driven by climate warming, indicating that climate can effectively replace eutrophication as principal driver (Bruel *et al.*, 2018). Because local management policies and human activities vary among those lakes, the hypothesis that local human impact may modulate the ecological vulnerability to climate warming has been suggested (Perga *et al.*, 2015). Should the local management decision modulate the vulnerability to climate, this could motive politics to undertake more ambitious preservation programs. On the other hand, if geomorphological parameters emerge as a potential factor of vulnerability, this could help to target ecosystems on which preventions programs and research on adaptive biology shall be prioritized.

The difficulty of predicting biological responses to climate warming may come from at least two aspects. First, the general lack of regional coherence of biological responses comes from the number of local filters that interfere with the global signals (Livingstone *et al.*, 2010). These filters include the altitude, the geomorphology, and the specific land use on watershed and interfere with the sole climatic signal. For instance, high lake/watershed surface area ratio increases their buffering capacity nutrient loads. Good connection of wastewaters to efficient treatment plants decreases the stress from cities development on ecosystems. A small lake with high water residence time that receives important loads of poorly treated waters is more likely to turn eutrophic. Secondly, some systems may have come off from their original trajectory, shall they have undergone a critical transition and are now in an alternative stable state with different vulnerability. In lakes, alternative states are often maintained by the presence or absence of macrophytes (Carpenter *et al.*, 2001; Hilt, 2015). Only a reduced zone than can support such habitat in deep lakes, which make them less prone to such transition. However, regime shift may take place at a spatial scale, and a threshold may be reached for lower and narrower nutrient levels in deep lakes than in shallow systems (Scheffer & van Nes, 2007; Janse *et al.*, 2008; Bruel *et al.*, 2018). In the new state, different forces may drive the vulnerability to climate, which would eventually hamper drawing a general scheme of expected responses across lakes.

Resilience is an emergent property of systems that maintain them stable over long period of times thanks to internal feedbacks (Hodgson, McDonald & Hosken, 2015). It is a desirable property of healthy ecosystems, but an unprofitable characteristic of degraded ecosystems (Lake, 2013). Indeed, managers must juggle between enhancing and eroding resilience depending on the state of the system when measures are undertaken. In fact, the methods to quantify recovery (e.g. variance, Burthe *et al.*, 2015) are rarely reproducible among systems. Measuring resilience of ecosystems is topical but faces many difficulties. Some qualitative approaches aimed at stakeholders have been developed (e.g. Nemec *et al.*, 2014), but are not always adapted to address multiscale structures. Finally, quantitative approaches were developed to characterize ecosystems dynamics before abrupt changes, in the hope to develop early warnings of transitions (Carpenter & Brock, 2006). However, early warnings indicators sometimes fail to predict critical transitions (Burthe *et al.*, 2015), and their use require long-term and/or high-frequency datasets to disentangle the early warnings from the natural ecosystems variability (Spears *et al.*, 2017).

Previous attempts to compare the phytoplankton community responses to eutrophication and climate warming of deep lakes were undertaken but soon confronted to the difficulty of generalizing results among lakes (Gallina *et al.*, 2013). Herein, we provide our own attempt of quantifying ecological vulnerability of peri-alpine lakes. We work on a greater number of lakes than Gallina *et al.* (2013) (12 vs. 6), on a longer period of time (110 years vs. 23 years), and our focus was on different planktonic groups (zooplankton here vs. phytoplankton in the Gallina *et al.* (2013)'s study). Should our attempt be successful on the lakes of our dataset, results should be widened at a larger scale. Regarding the long-term recoil, we consider it as an important factor as climate forcing is a long-term forcing. Yet, we suggested previously that eutrophication might have acted as a vulnerabilizing factor of lakes, making their ecology more sensitive to climate warming (Bruel *et al.*, Under Review). In other words, while hydrodynamics processes are explained by local settings and climate (O'Reilly *et al.*, 2015), ecological trajectory can be decoupled from these sole parameters. Since the timing of eutrophication varies among lakes, we standardized the situation by resetting our datasets from

1900. On the other hand, we could not grasp seasonal variability from our data. Gallina *et al.* (2013) showed that both climate and eutrophication had an important role during the growing season but not during the grazing season. They found a good coherence of such a signal across lakes, so that our results should not be impacted by our annual integrative approach. Finally, phytoplankton assemblages are strongly responding to the eutrophication gradient (Bennion, Simpson & Goldsmith, 2015b). Because our objective was to quantify climate vulnerability, we focused on Cladocera, a micro-crustacean family that displays responses to climate variability (Alric *et al.*, 2013; Bruel *et al.*, 2018).

## 6.3 | MATERIALS AND METHODS

### 6.3.1 | STUDY SITES

Twelve peri-alpine lakes located in Italy, France, and Switzerland, were included in the study (Figure 6.1). The lakes cover a large range of trophic states, are located at different elevation (65-1004 m asl, average 375 m asl) and vary greatly in size (z= 26-350 m, Table 1). They display contrasted residence time and lake/watershed surface area ratios. Sediment cores were retrieved from the deepest points of their pelagic zones and dated resorting to radionuclides dating method and/or varves counting. The sediments records covered 40 to >200 years. More details about coring and dating are given in Chapter 2.

### 6.3.2 | CLIMATE

The climate of the region is subcontinental temperate, with warm and dry summers and cool and wet winters. Datasets of mean annual air temperature (MAAT) were extracted from the gridded HISTALP dataset for Italian lakes (Auer *et al.*, 2007), according to lakes geographical coordinates for the time period covered by the sedimentary records (1837-2010). For French and Swiss lakes, monthly temperature were retrieved from the MeteoSwiss database and averaged over the year. All MAAT data were converted to MAAT anomalies using 1961-1990 as the reference baseline.

### 6.3.3 | INFERRED WATER [TP]

For most lakes, only punctual TP measurements were available. The mean total phosphorous (TP) concentrations were reconstructed using diatom and pigment-based inference models (I-TP) for eight lakes. References of published transfer functions can be found in Table 6.1. Figure 6.2 shows TP (inferred or monitoring data when available) versus MAAT.

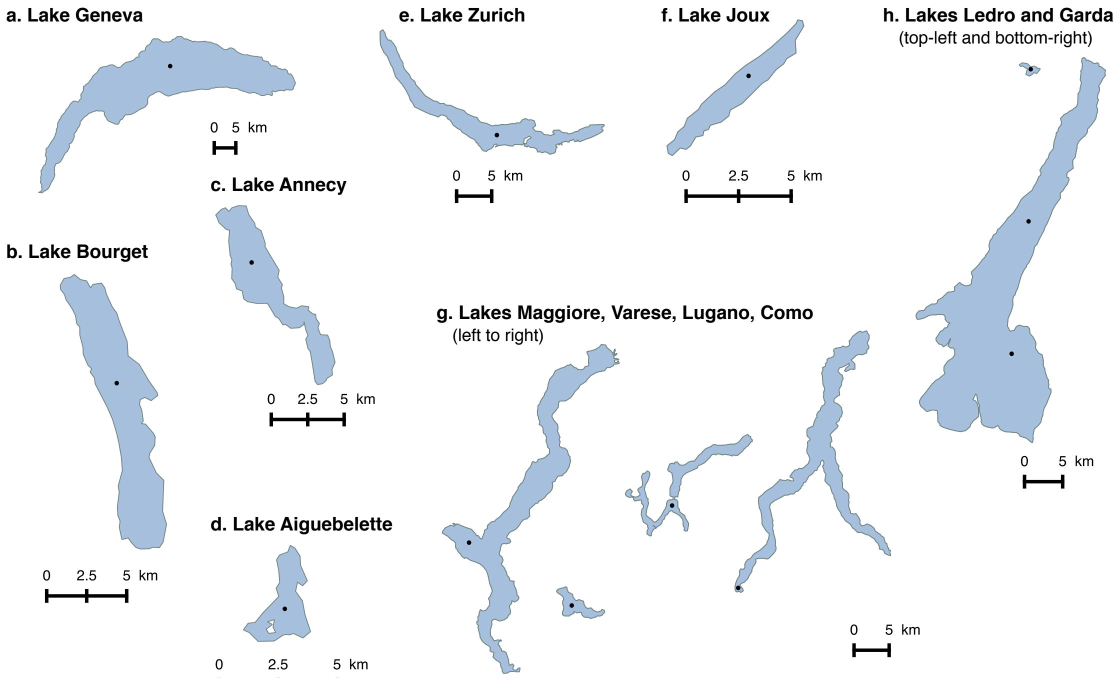

**Figure 6.1 I** Study sites; dots indicate the coring locations.

(a) Lake Geneva, CH, FR, (b, c, d) the French lakes, Lakes Bourget, Annecy and Aiguebelette), (e, f) the Swiss lakes, Lakes Zurich and Joux, (g) the Italian lakes of the Insubrian Southern Alps and pre-alps, Lakes Maggiore (CH, IT), Varese, Lugano (CH, IT) and Como, with the actual distance between them kept as it is, (h) the Italian lakes at the East of the study area, Lakes Ledro and Garda, with the same scale. Lake Garda was sampled in two basins, Brenzone (Northern deepest basin) and Bardolino (Southern basin).

### 6.3.4 | SUBFOSSILS CLADOCERA

Cladocera were used as the proxy for ecological state. The sources of previously published dataset are given in Table 6.1. New cladoceran sequences were analyzed according to Frey (1986). > 400 cladoceran remains were counted and identified per sample (headshields, shells, post-abdomens, post-abdominal claws, mandibles and others) using the determination keys of Szeroczynska and Sarmaja-Korjonen (2007) and an Olympus BX41 microscope at 100-200 magnification. *Bosmina* were determined to the species level (*B. longirostris*, *E. longispina*, and *E. coregoni*), as well as chydorids, whenever possible. Given their taxonomic complexity, *Daphnia* spp. were identified to the genus level. The evolutions of cladoceran assemblages for the different lakes are presented in Chapter 2.

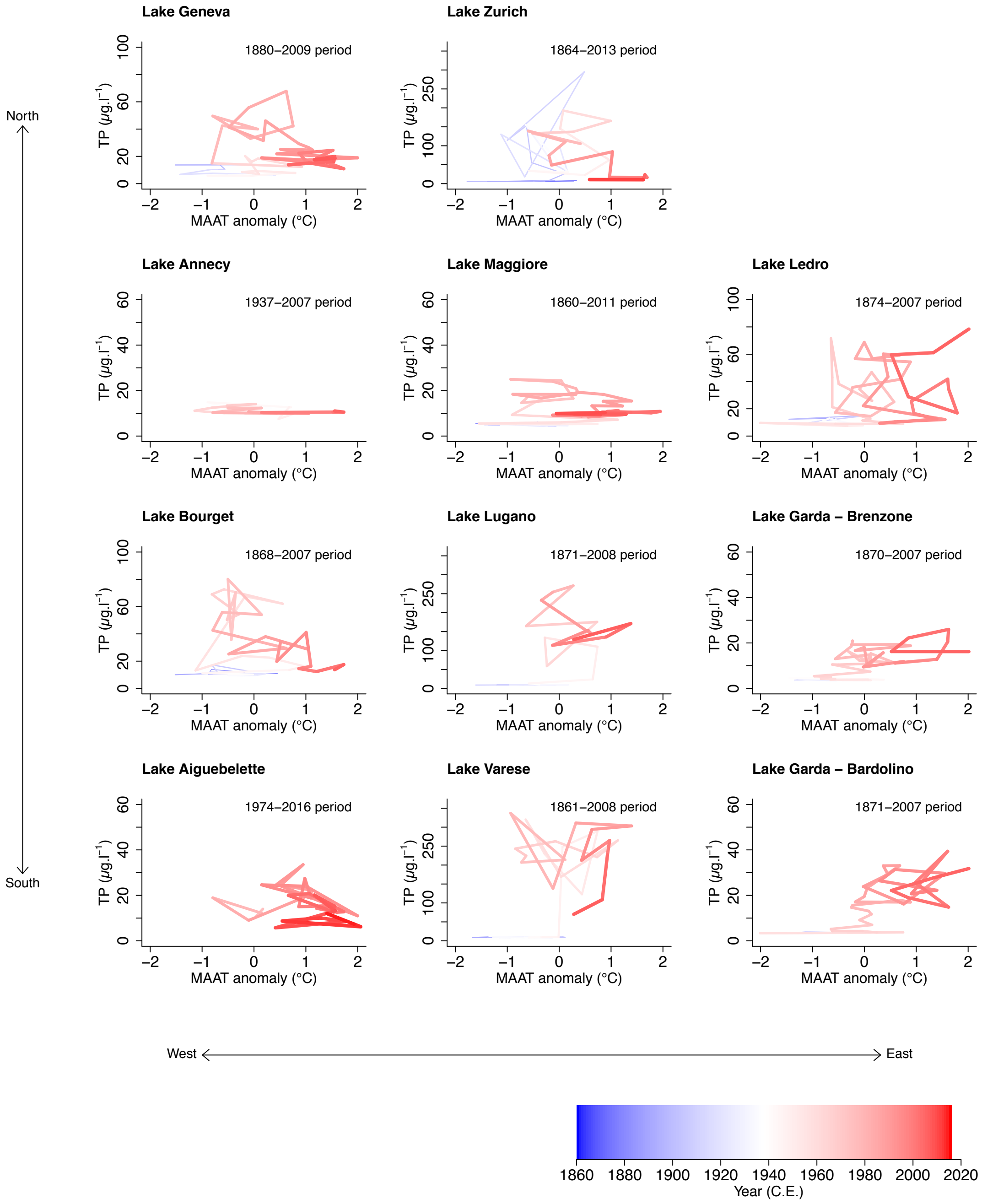

**Figure 6.2 I** Total phosphorus (TP) versus mean annual air temperature (MAAT) anomalies for 10 lakes of the study, classified roughly along their North/South and West/East gradients.

While all lakes underwent eutrophication over the last 50 years, with yet different extents, there is a differential timing compared to atmospheric warming, i.e. Lakes Geneva, Bourget and Aiguebelette went back along a re-oligotrophication trajectory in the recent warming period, while in Lake Garda, the eutrophication and the warming trend are correlated. No long-term data were available for Lake Como (IT) and Lake Joux (CH). The colour gradient indicates the time period.

**Table 6.1 I** Lakes characteristics.

There are two values of TP for Lake Garda for the two basins, Brenzone and Bardolino.

| Lake (country code) | **Information about the lake** | | | | | | **Information about sediment record** | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Coordinates (Long. / Lat.) | $z_{max}$ ($z_{mean}$) | Lake (watershed) surfaces area (km$^2$) | Elevation (m a.s.l.) | TP in 2010 (max TP) ($\mu$g.l$^{-1}$) | Period covered | Sub-sampling interval | Dating | TP reconstruction | Reference |
| Aiguebelette (FR) | 5.53530 / 45.45492 | 71 | 5.45 (70) | 373 | 10 (>35) | 1833-2008 | 0.5 cm | Radionuclides ($^{137}$Cs, $^{241}$Am, $^{210}$Pb$_{ex}$) | - | New data |
| Annecy (FR) | 6.16442 / 45.86858 | 82 (40) | 27 (251) | 447 | 7 (25) | 1862-2005 | Facies (<1 cm) | Radionuclides ($^{137}$Cs, $^{241}$Am, $^{210}$Pb$_{ex}$) | DI-TP | (Perga *et al.*, 2010; Berthon *et al.*, 2013) |
| Bourget (FR) | 5.86257 / 45.73662 | 145 (80) | 180 (560) | 232 | 10 (110) | 1864-2005 | Facies (<1 cm) | Radionuclides ($^{137}$Cs, $^{241}$Am, $^{210}$Pb$_{ex}$) confirmed by varves counting | DI-TP | (Berthon *et al.*, 2013; Alric *et al.*, 2013) |
| Como (IT) | 9.266111 / 45.994444 | 410 (154) | 460 (4509) | 198 | 26 (75) | 1971-2009 | 1 cm | Radionuclides ($^{137}$Cs, $^{241}$Am, $^{210}$Pb$_{ex}$) | - | New data |
| Garda (IT) | 10.625 / 45.555278 | 346 (136) | 369.98 (2260) | 65 | 24 & 41 (24 & 41) | 1903-2008 | 0.5-2 cm | Radionuclides ($^{137}$Cs, $^{241}$Am, $^{210}$Pb$_{ex}$) | DI-TP | (Milan *et al.*, 2015, 2017) |
| Geneva (CH, FR) | 6.51742 / 46.44267 | 309 (152) | 730 (7395) | 372 | 25 (90) | 1852-2008 | Facies | Radionuclides ($^{137}$Cs, $^{241}$Am, $^{210}$Pb$_{ex}$) confirmed by varves counting | DI-TP | (Berthon *et al.*, 2013; Alric *et al.*, 2013) |
| Joux (CH) | 6.285833 / 46.639444 | 32 (21) | 8.77 (211) | 1004 | 12 (>35) | 967-2016 | 1 cm | Radiocarbon and radionuclides (Lavrieux *et al.*, 2017) | - | New data |
| Ledro (IT) | 10.75056 / 45.87667 | 58 (35) | 2.19 | 655 | ~40 (78) | 1600-2011 | | Radionuclides | DI-TP | (Milan, Bindler & Tolotti, 2016)6) |
| Lugano (IT, CH) | 8.58 / 45.59 | 288 (132) | 48.7 (565.6) | 271 | 60 (170) | 1638-2008 | 1 cm, removing any instantaneous event | Radionuclides ($^{137}$Cs, $^{241}$Am, $^{210}$Pb$_{ex}$) | DI-TP | New data |
| Maggiore (IT, CH) | 8.5825 / 45.905 | 372 (177) | 212.5 (6599) | 193 | 12 (25) | 1943-2010 | 1 cm | Radionuclides ($^{137}$Cs) | DI-TP | (Marchetto *et al.*, 2004; Nevalainen, Brown & Manca, 2018) |
| Varese (IT) | 8.733333 / 45.816667 | 26 (11) | 14.5 (112) | 238 | 70 (337) | 1837-2010 | 1 cm | Radionuclides ($^{137}$Cs, $^{241}$Am, $^{210}$Pb$_{ex}$) confirmed by varves counting | Composite I-TP diatoms and pigments | (Bruel *et al.*, 2018) |
| Zurich (CH) | 8.683333 / 47.25 | 136 (49) | 88.66 (1829) | 406 | 35 (110) | 1845-2017 | 1 cm | Varves counting | DI-TP | New data |

### 6.3.5 | STATISTICAL ANALYSES

The impacts of climate change are likely overridden by the local human impacts (Parmesan & Yohe, 2003). As a result, as local human impacts fluctuate, we do not necessarily expect a monotonic response. Species may display multi-modal distributions as a response to several forcings. A preliminary literature survey failed in identifying a method that could fill our requirements. We needed to compare ecological responses to climate warming (1) across systems and (2) for complex dynamics (not necessarily specie appearance, disappearance). Most methods applied to several systems are either qualitative, either designed to detect one trend (e.g. cyanobacteria dominance, Taranu *et al.*, 2015; Monchamp *et al.*, 2017). To fill the gap, we propose thereafter a method to quantify lakes ecological vulnerability to change in MAAT, using quantitative tools usually applied for one single system. Data aggregation and statistical analyses were performed using R version 3.1.2 (2014-10-31, R Core Team, 2014), as well as the packages cited below.

#### 6.3.5.1 | Summary of the variability at the organization level

Multivariate ordination methods are powerful tools to summarize the variability in an assemblage along one or several gradients into a restricted set of univariate data (i.e. principal components). As a consequence, in most cases, it is relevant to select more than one axis to fully apprehend the ecosystem variability (Bruel et al., Under Review, Chapter 5; Bennion et al., 2015b; e.g. Bruel et al., 2018, Chapter 4). In here, we used principal component analysis (PCA). PCA were fitted using the package vegan (Oksanen et al., 2016).

#### 6.3.5.2 | Adjusting for irregular sampling

The time density of observations varied strongly among and between cores. To account for this limitation, we interpolated linearly from point to point the raw data. This choice was also made because we later used general additive models (GAM) that cannot fit relationships when there are too little observations. In order to make sure the data were not overly simplified and degraded by this process, we computed two independent PCAs, on the raw and on the interpolated dataset. The ordination on the first factorial plan was not affected by this step. When we later performed additive models, we authorized the use a continuous time first-order autoregressive (CAR(1)) process for the residuals, to account for the lack of independence between the observations (Simpson & Anderson, 2009; Bennion *et al.*, 2015b). The choice to include or not the correlation structure was conducted using the log-likelihood of each model (package “mgcv”, Wood, 2016).

#### 6.3.5.3 | Quantifying vulnerability

The main challenge to overcome was to find a way to compare quantitatively the vulnerability of several lakes to climate change, i.e. to quantify the amount of ecological changes that was unequivocally attributed to atmospheric warming. Thereafter, and following our findings of Chapter 5 (Bruel *et al.*, Under Review), we defined vulnerability as the quantified response to a specific driver. Because we know that local human impact may have modified lakes vulnerability to climate variability (Bruel *et al.*, Under Review), we ran the analysis only for the 1900-2010 period in order to get a similar time frame, under the hypothesis that changes in TP was the most symptomatic evidence for local human impacts. This hypothesis was confirmed by including I-TP and MAAT for the eight lakes with available I-TP. Ideally, our objective was to quantify the changes due to MAAT without resorting to I-TP. It would make feasible to extend our analyses to more lakes across and/or outside the alpine region.

Linear and additive models, by essence, cannot deal with any potential bistability. As a result, the recent climate variability can be hidden by the weight of the previous record during which the climate vulnerability was lower (see Bruel *et al.*, Under Review for example). We used GAM to quantify the contribution of the driver to the variability in the assemblage for the selected period i.e. 1900-2010 (Figure 6.3 b and f). This time frame ruled out two lakes from our analysis, Lakes Como and Maggiore, whose records covered less 45 and 70 years respectively.

Then, if the driver (i.e. atmospheric warming) explains well the variability of the state variable, we conclude that this state variable is vulnerable to the driver. Vulnerability is quantified as the percent variance explained by atmospheric warming, as explained by the model.

Figure 6.3 summarizes the principle of the analysis. We ran GAM using MAAT as covariate to explain the variability in the two first components of the PCA. The percentage of variability explained by GAM is a proxy for the vulnerability or sensibility of the dependant variable (i.e. cladoceran assemblage) to the independent variable (i.e. forcing, MAAT). If the percentage is low, it means that despite variations in the driver (MAAT), they are not driving modification in the cladoceran assemblage. On the other hand, if the percentage is high i.e. MAAT is explaining a large part of the variability in the cladoceran assemblage, then we concluded that the ecology of the lake was vulnerable to climate.

Yet, the systems have undergone various levels of eutrophication for the period of interest, and not necessarily within the same time frame. The risk of false positive (i.e. ecological changes attributed to climate warming instead of TP) was high when the timing of warming coincided to the timing restoration as in Lake Geneva, or to the timing of eutrophication as in Lake Garda (Figure 6.2). On the other hand, false negative could occur if the level of phosphorus stayed high but climate is still moving the ecological state further away from its equilibrium.

To tackle this issue, we ran a second and third sets of GAM, using both TP and MAAT anomalies as covariates (Figure 6.3 c and g), and then only TP (Figure 6.3d and h). Then, we subtracted the results obtained between the two models in order to get the vulnerability only due to MAAT anomalies (Figure 6.3 e and i). The contribution of climate (apprehended by MAAT anomalies) to the variability observed for each species was calculated with this method. We obtained two values of vulnerability (for PC1 and PC2 respectively). For each method, we only kept the maximum deviance explained. This approach was possible only for the lakes with available TP data i.e. 9 of them, including Lake Garda for which two cores were available.

In the sketch (Figure 6.3), including TP or not changes the selected axis from PC1 (considering only MAAT) to PC2 (if both MAAT and TP are considered). In case MAAT increase coincided with TP dynamics (for instance, re-oligotrophication occurs at the same time that air temperatures warm up), the model could erroneously attribute a large range of explained deviance to MAAT while TP is driving the ecological changes. With no further insight, and using blindly our method, we could have selected PC1 as the axis carrying climate driven changes.

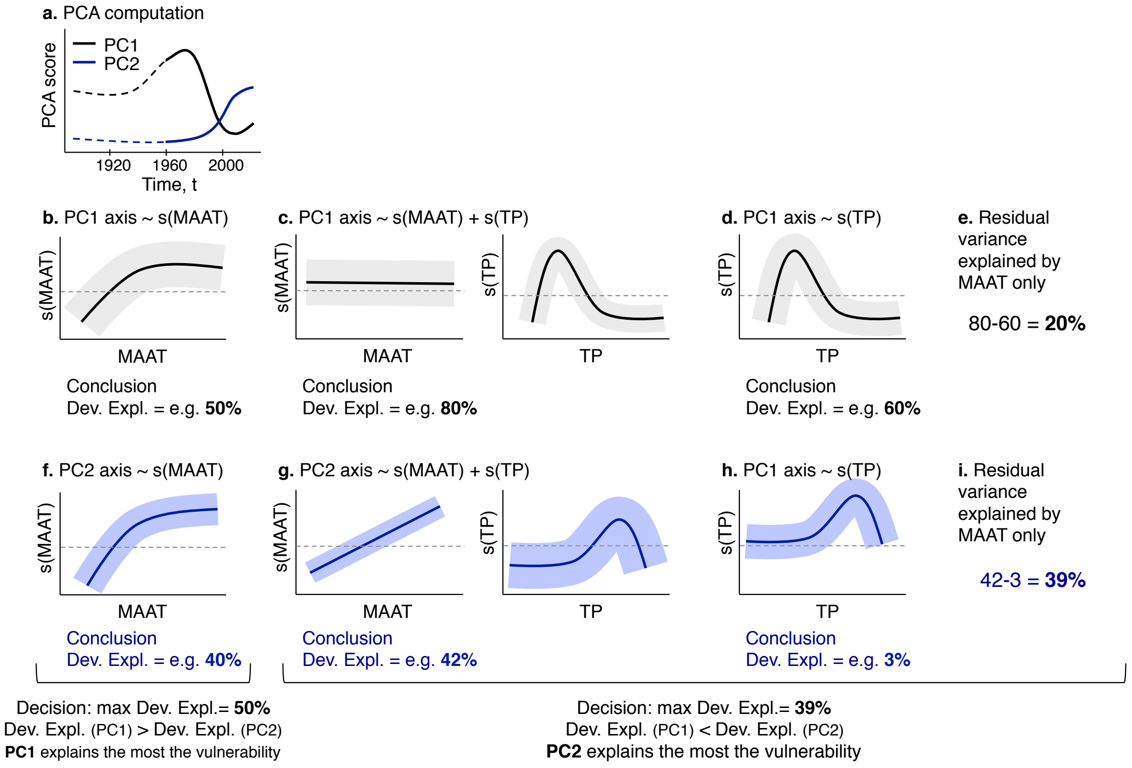

**Figure 6.3 |** Steps of the analysis to identify ecological vulnerability to air temperature changes.

(a) We summarized the variability in the cladoceran assemblage into principal components (PC) for each lakes. We selected the 1900-2010 period for each lake (plain line). (b to i) General additive models (GAM) with smooth terms computed for PC1 (grey) and PC2 (blue). We extracted the deviance explained (Dev. Expl.) for each covariate ((b, f) mean annual air temperature – MAAT, (d, h) total phosphorus – TP, and (c, g) combination of both). (e, i) We extracted the variance explained solely by MAAT by subtracting the Dev. Expl. for the c and g scenarios (MAAT + TP) with the Dev. Expl. for the d and h scenarios (only MAAT). For each method, (b, f) and (e, i), we selected the maximum explained deviance.

To sum up, we based our analysis on three hypotheses. (1) Lake ecological vulnerability to an external driver is computed as the amount of variability of a state variable that can be explained by this external driver, regardless the shape of the underlying relationship (Simpson & Anderson, 2009). (2) A model's performance can be affected by the number of points used in the fitting, i.e. less data points can result in better fit until a threshold is met, when there are not enough data points to fit any model. To tackle this issue, a yearly resolution for each system was reached running linear interpolations from the raw dataset. We justified this choice because the composition of the assemblage, rather than the abundance of each individual species are used to build PCA. However, the degraded signal would not account accurately for abrupt transitions, which was yet not part of our question. (3) Based on our previous findings on Lake Geneva, we assumed that even though large lakes regime of vulnerability may have changed over the past century (Bruel *et al.*, Under Review), it should have been stable since early levels of eutrophication have been crossed. Thereby, all lakes were considered to be within their human altered regime of vulnerability to climate change for the 1900-2010 period.

#### 6.3.5.4 | Explaining vulnerability

Many studies on climate warming impacts focus on lakes physical responses e.g. surface water temperature or the length of the stratification period (O'Reilly *et al.*, 2015). Their findings identify geomorphological features as important drivers of inter-lakes variability (Livingstone & Padisák, 2007; O'Reilly *et al.*, 2015). If physical vulnerability is important for ecological vulnerability, then geomorphology should come out from the analysis as the main explanatory variable. On the other hand, if local human impact is revealed as an important vulnerabilizing factor, then we should find some local impact metrics (TP) to be important.

For each lake, we listed geographic coordinates, altitude and morphometric parameters (maximum and mean water depth, lake and watershed areas, lake perimeter). We also calculated some lake descriptors the relative depth ($Z_r$) and the development of volume ($D_v$) that are two measures of the shape of a lake. $Z_r$ is the maximum depth as a percentage of mean diameter defined as:

$$Z_r = 50 \times Z_{max} \times \sqrt{\pi} \times \sqrt{A_0}^{-1};$$

where $Z_{max}$ is the maximum depth, $A_0$ the surface of the lake, and $Z_r$ is expressed in percentages (Hutchinson, 1957; Wetzel & Likens, 1991). $Z_r < 2\%$ for most lakes, but deep lakes with small surface areas have higher relative depth. $D_v$ is a measure of departure of the shape of the lake basin from that of a cone (Hutchinson, 1957) and is calculated as follow:

$$D_v = 3 \times {}^{Z_{mean}}\!/_{Z_{max}};$$

$D_v > 1$ for the majority of lakes (i.e. conical depression) and reaches greater values for shallow lakes with flat bottoms and deep lakes.

Indicators of anthropogenic perturbations were estimated through levels of eutrophication (maximum TP, average TP over the past 20 years, TP in 2010), retrieved from long-term monitoring programs whenever possible, as DI-TP could overestimate the maximum levels. Once we obtained scores of vulnerability, we ran correlation analysis and linear regression models, with and without interactions, to identify the main explanatory variables for the discrepancy in climate vulnerability. Residuals were checked for normality and homogeneity of variance.

We ran non-linear least squares (*nls*) analysis to estimate the parameter of non-linear model. We repeated the analysis 100 times, resampling 10 out of the 11 lakes, to get average estimates of models parameters.

## 6.4 | RESULTS

### 6.4.1 | COMPARISON OF LAKES ECOLOGICAL TRAJECTORIES

Three scenarios of eutrophication were observed in the sample of lakes we got to study herein. Lake Zürich displays an original eutrophication trajectory, as it was the first one to turn eutrophic as soon as the late 19th century. A second wave of eutrophication took place in the second part of the 20th century, following the end of World War II. The lake is now on a restoration trajectory. The second scenario of eutrophication applies to almost all the lakes of the peri-alpine region (Lakes Aiguebelette, Annecy, Bourget, Geneva, Joux, Lugano, Maggiore, Varese). Theses lakes underwent first changes in nutrient levels most likely in the 1920s-1930s, as revealed by the increased abundance in *Daphnia* spp., that appeared as a good indicator of early eutrophication stages (Alric *et al.*, 2013; Bruel *et al.*, 2018). For these lakes, eutrophication intensified right after WWII. Thereafter, depending on the presence or absence of early managements decisions but also some factors directly linked to the land use and population density on the watershed, lakes shifted to a meso- (Joux, Annecy, Aiguebelette) or to a eutrophic (Bourget, Geneva, Lugano, Zurich…) state. From the late 1970s and until the 1990s, all lakes managers adopted management practices that could restore lakes water quality. The extent of maximum P level varies greatly among systems (Varese > Lugano > Bourget >

Geneva > Joux > Aiguebelette > Annecy), and the current P mirrors this distance between oligotrophic and eutrophic state, as Lakes Varese and Lugano were still eutrophic in the 2010s. Finally, the last scenario of eutrophication concern Lakes Ledro and Garda. These two lakes located at the Eastern part of our study site are still on a eutrophication trajectory (Figure 6.2), as they are on a late development hotspot of urban extent (Kuemmerle *et al.*, 2016). As a result, the effects of eutrophication may override the effects of climate warming, or instead reinforce their vulnerability to climate change.

## 6.4.2 | QUANTIFICATION OF VULNERABILITY

The first factorial plan of the PCA explained between 35% (Varese) and 80% (Annecy) of the total variance in the dataset (Figure 6.4). Lakes Varese and Zurich were the only two lakes for which less than 50% of the total variability was carried out on the two first axes.

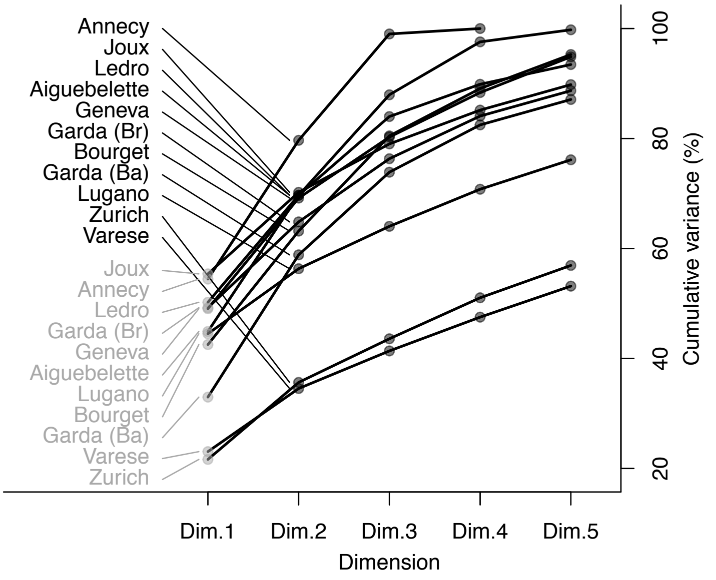

**Figure 6.4 I** Cumulative variance explained for the first 5 dimensions of the principal component analyses (PCA) computed for each lakes.

Lakes are ranked according to the maximum variance on the first dimension (grey) and the cumulative maximum variance on the second dimension (black).

We compared the scores of vulnerability (Dev. Expl.) to MAAT variability for the 10 sites for which both MAAT and TP were available (9 lakes, 2 cores in Lake Garda). The ranking between of lakes according to their vulnerability with solely MAAT as covariate was really different from the one using MAAT and TP. For instance, MAAT could explain up to 37% of the variability on the first dimension (46%) of Lake Lugano assemblage (Figure 6.5). However, the changes on this axis were directly linked to change in TP levels as confirmed by the really good performance of the models including solely TP or both drivers. By extracting the residual variance explained solely by MAAT on the two first components (56% of the variability), we found scores close to 0 on both axis, indicating a very low contribution of air temperature on the lake. The case of Lake Lugano provides an example of false positive. PC1 ~ s(MAAT) could explain 30% of the variability. However, TP is a better predictor and explained 95% of the variability.

In Lake Varese, hypereutrophication led to deep rearrangement for all the lake organisms (Ceccuzzi, 2008; Bruel *et al.*, 2018). The changes driven by TP were mostly found on axis 1 (Figure 6.6 d), while axis 2 carried modifications due to climate (Figure 6.6 g). However, left with only TP as covariate, GAM could still fit a relationship between PC2 and TP (Figure 6.6 h), which lower the final residual score (Figure 6.6 i). If we calculated the residual explanation of TP as covariate on PC2, we would obtain solely 4%, which confirm that TP is driving modifications on PC2 in a lesser extent.

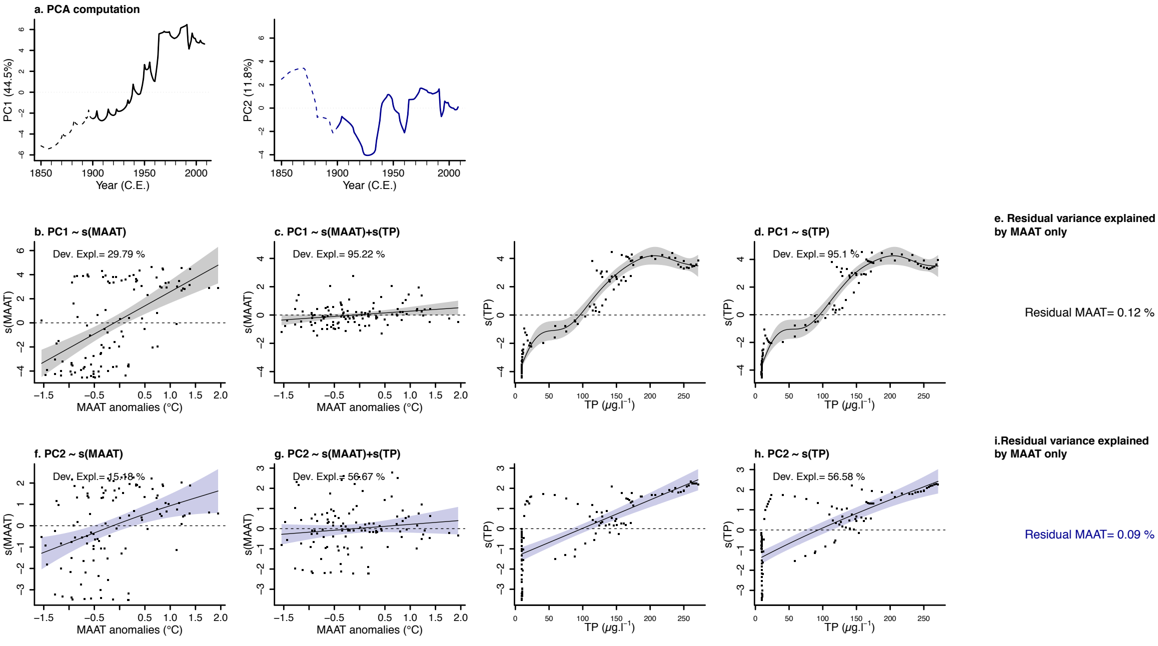

**Figure 6.5 I** False positive on axis 1.

Same as Figure 6.3, but with real data from Lake Lugano. From the PC axis (a), three separate GAM models were computed for PC1 (b, c, d) and PC2 (f, g, h).

Concomitancy of reoligotrophication and climate warming is the explanation for the good score of MAAT on explaining PC1. This showcased how the exclusion of the major role of TP in structuring lake communities may drive false positive.

On the other hand, the maximum climate driven changes on any PC were well correlated to the variance due to climate change on axis 2 (Spearman rho=0.67, p-value < 0.003, Figure 6.7). Similarly to what has been observed in shallow lakes, if the main driver of zooplankton assemblages is TP, climate popped up as the second most important (Gyllström *et* *al.*, 2005). In multivariate analysis, axes orthogonal property allows a good separation of the modification in the assemblage. PC1 carried most of the variability due to changes in TP. We used PC2 as the main climatic gradient and could include the lakes for which long-term I-TP were not available i.e. Lakes Joux and Aiguebelette, and provided the ranking in vulnerability (Figure 6.7).

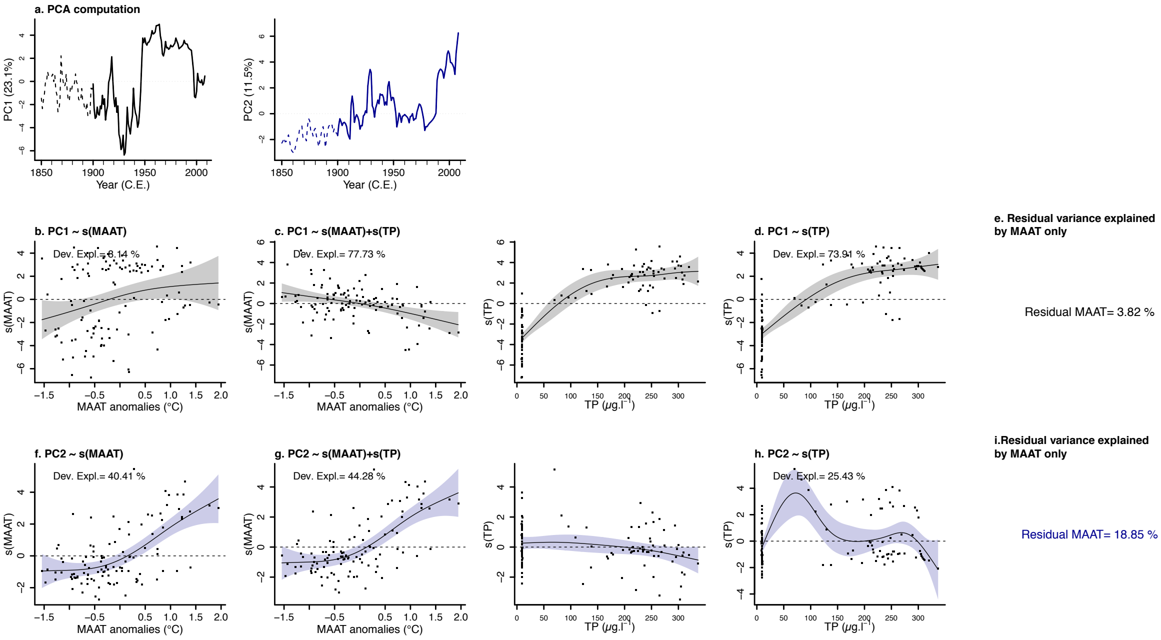

**Figure 6.6 I** False negative on axis 2.

Same as Figure 6.3, but with real data from Lake Varese. From the PC axis (a), three separate GAM models were computed for PC1 (b, c, d) and PC2 (f, g, h).

The method hierarchized well Lakes Annecy, Bourget and Geneva, lakes for which ecological processes were studied in depth (see synthesis in Perga *et al.*, 2015). We were indeed expecting to find a lower vulnerability for Lake Annecy, a maximum vulnerability for Lake Bourget, and an intermediate vulnerability for Lake Geneva. We then confronted the scores of vulnerability to the potential explanatory variables.

The scores obtained on the first two axes were transformed ($\times(-1)$ or $\times 1$) so the dynamics would be comparable i.e. positive during the 1960-1980s on axis 1 (mostly carrying the variability due to local human impact) and positive from the 1990s on axis 2 (mostly carrying the variability due to global impact. Then species contributions to the two first axes were extracted for each lake (Figure 6.8). Species which loadings > 0.2 were considered as significantly represented on PC . On axis 1, periods with positive scores (at least the 1960-1980 period based on our filtering) were characterised by *Bosmina* sp. and the large macrophyte associated species *Sida crystallina*. Periods with negative scores were characterised by *Bosmina longirostris* and the larger *Daphnia* spp, but also by several littoral taxa, both macrophyte associated (*Alonella excisa, Acroperus harpae, Eurycercus*) and sediment associated (*Alona affinis, Monospilus dispar*). The shapes of the violin plots are markedly different between negative and positive loadings. It indicates that years with negative scores on axis 1 are generally characterised by several species while globally less species are really abundant during the 1960-1980 period. However, this could also come from the large unbalance of diversity between pelagic and littoral taxa. On axis 2, years with positive scores (at least the recent-most period, >1990), the assemblage of 7 lakes (out of 10) were characterised by the presence of *Eubosmina longispina*. Other redundant species across lakes include *Eubosmina coregoni, Leptodora kindtii*, *Daphnia* spp., and in a lesser extent *Bythotrephes longismanus.* To summarise, pelagic grazers (*Eubosmina* sp. and *Daphnia* spp.) and predator (*L. kindtii*) dominate the recent assemblage. Negative scores on axis 2 are characterised by pelagic grazers *Daphnia* spp. and *Bosmina longirostris*, as well as littoral taxa with ubiquitous requirements (sediment and/or macrophytes) *Chydorus sphaericus, Alona rectangula,* and *Alona guttata*.

The presence of *Daphnia* spp. in every group may reflect the presence of different species. The hybridation processes make difficult evaluating which specie is present (Alric *et al.*, 2016). Rising phosphorus levels allowed the introgression of *Daphnia galeata* in the species

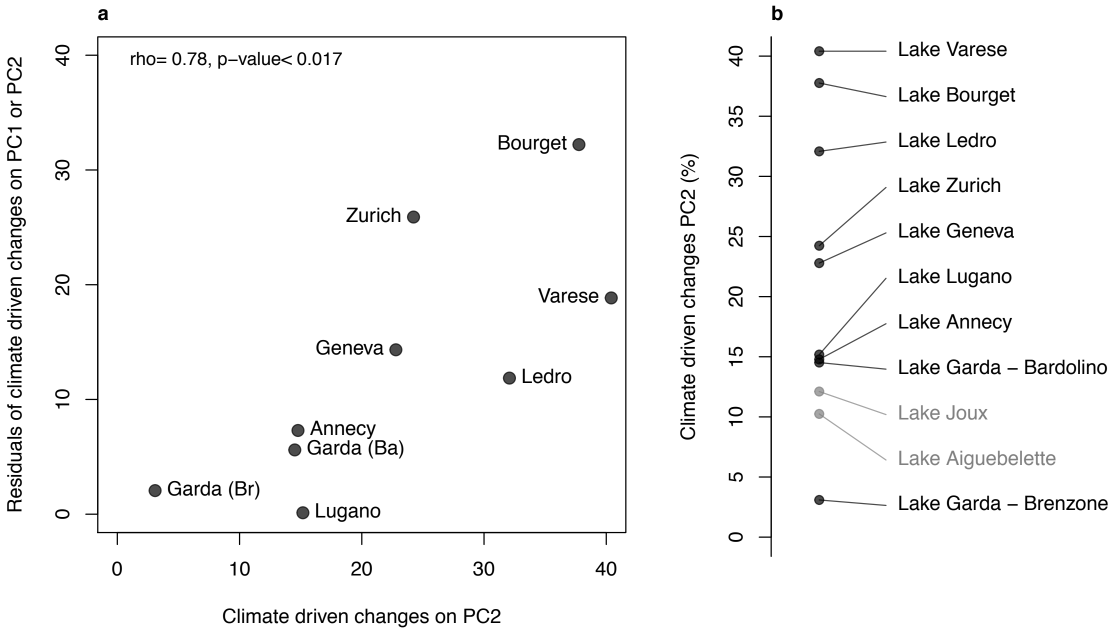

**Figure 6.7 I** Ranking of lakes according to their vulnerability to MAAT anomalies.

(a) Maximum residual variance due to climate change on PC axes versus climate driven changes on PC2. Spearman rank correlation indicates a significant correlation of the ranking between (b) Ranking of lakes according to their vulnerability. Grey lakes are the 2 lakes for which we could not test the hypothesis that the deviance due to climate is found on PC2. Climate driven changes is the percentage of variance explained by mean annual air temperature according the additive model.

complex in Lake Bourget and Geneva. This species appear to require at least a meso-oligotrophic status to establish, which suggest that the conditions for its establishment were fulfilled in most of the lakes of this study, Lake Annecy and Maggiore being the exceptions. The impacts of such hybridation on ecosystems functioning are not well known, but result in complex genetic trajectories (Alric *et al.*, 2016). Furthermore, the dominance of *Daphnia longispina* in Swiss oligotrophic lakes at the north of the Alps contrasted with the presence of *D. galeata* in warmer and more productive Italian lakes at the south of the Alps (Keller *et al.*, 2008).

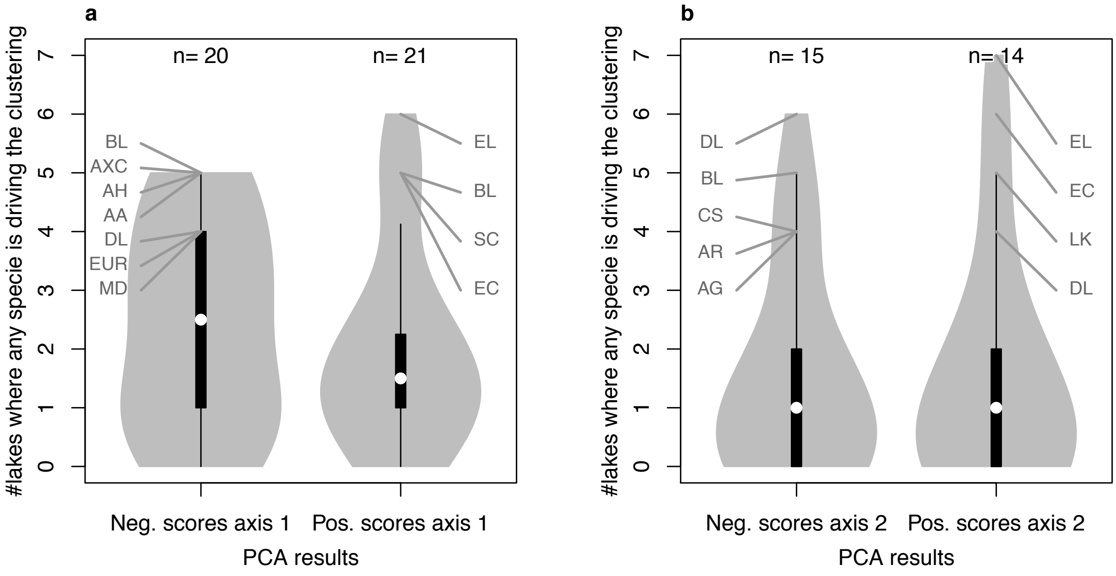

**Figure 6.8 |** Violin plots showing the probability density, median (white dot) and interquartile range of the number of lakes for which any of the n species (stated above each violin plot) contributed in driving the assemblage.

We only selected the species with coordinates >0.2 or <-0.2. A wide grey area means many species were found with that occurrence (on y-axis) across lakes. Plotted for (a) axis 1 and (b) axis 2 of the individual PCA computed for each lakes. PCA loadings are arbitrary. Data were transformed ($\times\mathbf{1}$ or $\times(-\mathbf{1})$) so the average scores during the 1960-1980 period would be positive on axis 1. The same transformation was carried out so the average scores during >1990 on axis 2 would be positive. For each PCA, we kept the species that contributed to the constructions of the axis. Then, we counted the occurrence of each species on each axis. This shows that the years with positive eigenvectors on axis 1 and 2 are more likely to be characterised by the same species than the years with negative eigenvectors on the selected axis. The species with the highest coordinates are indicated with their code. AA= *Alona affinis*, AG= *Alona guttata*, AH= *Acroperus harpae*, AR= *Alona rectangula*, AXC= *Alona excisa*, BL= *Bosmina longirostris*, DL= *Daphnia* spp., EC= *Eubosmina coregoni*, EL= *Eubosmina longispina*, EUR= *Eurycercus* sp., LK= *Leptodora kindti*, MD= *Monospilus dispar*, SC= *Sida crystallina.*

### 6.4.3 | EXPLAINING VULNERABILITY

We ran spearman rank correlation test and found the highest between the climate vulnerability and the average concentrations over the past 20 years (rho= 0.89, p-value= $2.58.10^{-4}$).

We then ran linear model using stepwise regression methods. The best model identified the average TP concentrations over the past 20 years as being the main drivers of ecological vulnerability to MAAT, explaining 51% of the deviance. The relationship with TP is weak (slope estimate= 0.19) but significant (p-value = 0.014) indicating that higher maximum levels of eutrophication increased the recent vulnerability to climate variability. When Lake Varese was removed from the equation, the relationship with TP dramatically increased (estimate= 0.64), so did the p-value (0.003). The data do not appear to be following a linear model.

We tested several model (linear, polynomial, sigmoidal) but the best performance was achieved with an hyperbole model was fitted to the model and converged in every situation with an average of 8 iterations (achieved tolerance= 3.85 $10^{-6}$). The parameters allowed fitting the model, as follow:

$$y = 63.5 \times x/(59.8 + x),$$

with x, the average TP concentrations over the past 20 years, and y, the quantity of response to MAAT. We performed a parametric correlation test between predicted and observed values and found that the data were significantly correlated (cor= 0.72, p-value= 0.012)

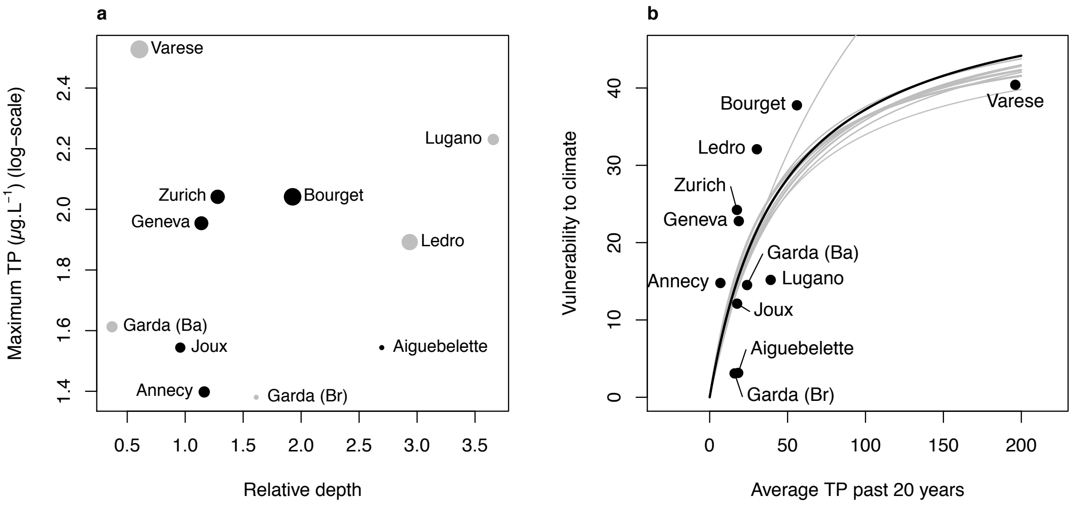

**Figure 6.9 I** Explaining lakes ecological vulnerability to MAAT anomalies.

(a) Maximum TP versus relative depth of the different lakes, with dot size proportional to vulnerability to climate. Black and grey dots are respectively for lakes North and South from the Alpine barrier. (b) Vulnerability to climate versus average TP over the past 20 years. Grey lines represent the 100 models fitted on a sample of the lakes (10 out of 11) and black line represent the average relation.

The relationship is non-linear as above ~50 µg P.L$^{-1}$, the vulnerability reached a plateau, although the lack of observational data between 60 and 200 µg P.L$^{-1}$, makes impossible to know the relationship in between (Figure 6.9).

Three levels of vulnerability can roughly be identified. Lake Aiguebelette and the pelagic zone of Lake Garda are showing the least response to MAAT variability; Lakes Annecy, Joux, Lugano and the southern basin of Lake Garda (Bardolino) display intermediate vulnerability; and Lakes Bourget, Ledro, Geneva, Varese and Zurich are the lakes with the greatest amount of variability explained by MAAT (Figure 6.10).

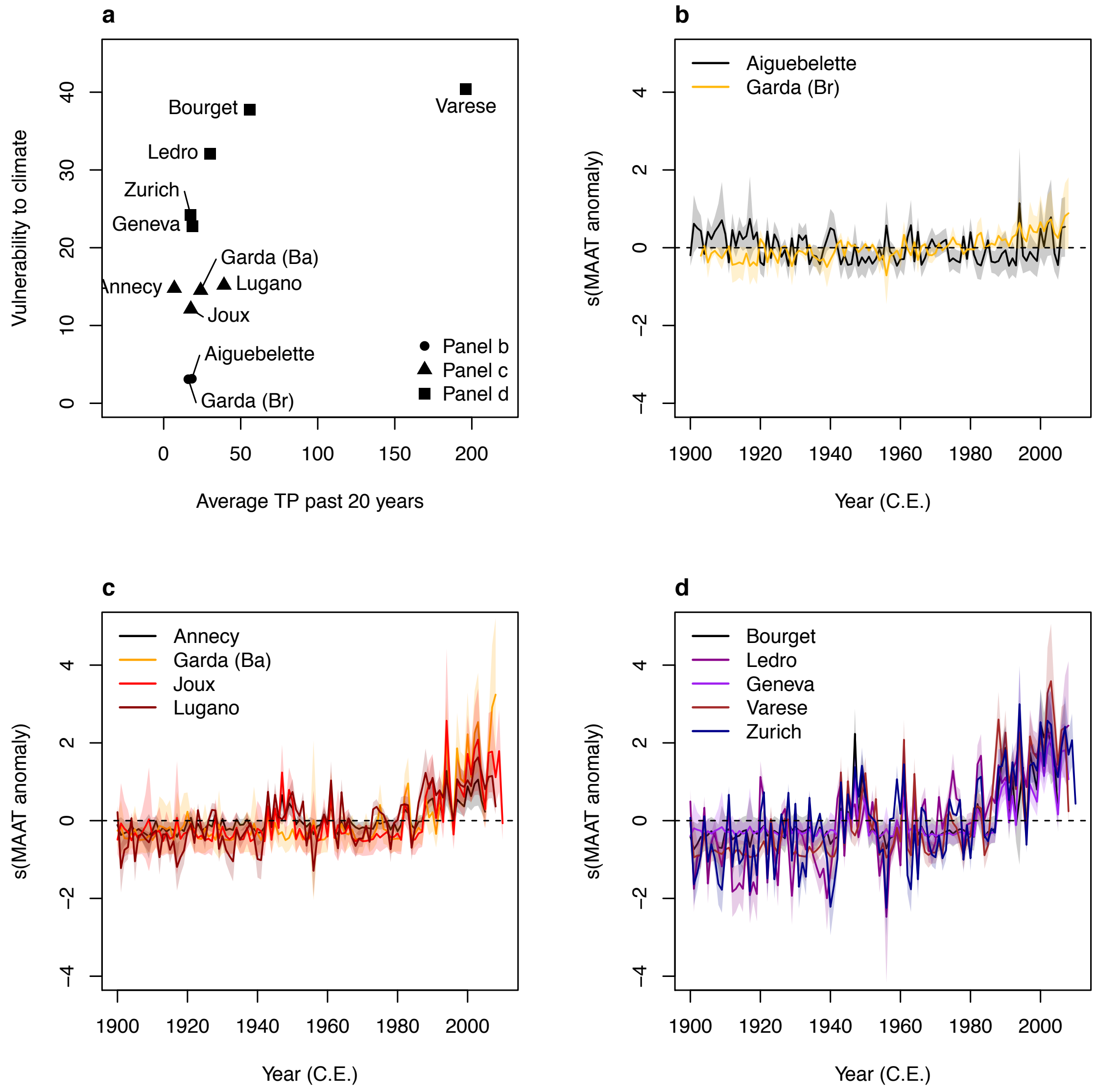

**Figure 6.10 I** Contribution of MAAT to ecological trajectories of the different lakes according to their vulnerability.

(a) Vulnerability to climate versus average TP over the past 20 years. (b-d) Predicted contribution of MAAT anomalies to assemblages of different lakes from low (b) to high (d) vulnerability.

## 6.5 | DISCUSSION

### 6.5.1 | PROBLEMATIC

Local human impacts have been the dominant drivers of ecosystems over the past century (Parmesan & Yohe, 2003). Energy flows, biogeochemical cycles and ecological corridors have been disrupted. Alongside, many ecosystems services were lost. In the meantime, global change has brought supplementary uncertainties into ecosystem management. In fact, similarly to the realisation that local drivers change the ecosystems services, the rapid change in climate may modify established equilibrium or limit the benefits of local restoration practices. One of the rare certitudes is that the projected increases in carbon dioxide and temperature over the next 50 years will substantially and very rapidly exceed the conditions Earth has been developing under over the past 100,000 years (Indermühle *et al.*, 1999; Meyer *et al.*, 2014). There are many uncertainties on how ecosystems will behave in the next decades as a response to climate warming. Herein, we investigate the driver of lakes ecological vulnerability to climate warming.

A vast majority of studies carried out on inter-lakes response to climate change are carried out on physical aspects e.g. water temperature or stratification (O'Reilly *et al.*, 2015). Those results point out the relative coherence of responses across lakes (Livingstone & Padisák, 2007), as long as correct morphometric variables are included (Toffolon *et al.*, 2014; O'Reilly *et al.*, 2015). In other words, for a similar exposure to climate warming, the geomorphology explains most of the variability in lakes thermal responses to air temperature. At the intra-annual scale, elevated mean depth in particular confers strong thermal inertia to lakes and increases the hysteretic pattern between air and lake surface temperatures (Toffolon *et al.*, 2014). At the inter-annual scale, this good coherence between air and lake surface temperature is best illustrated by the shift in temperatures in the late 1980s observed in alpine lakes (Woolway *et al.*, 2017), including Lakes Geneva and Zurich. It is worth noting that spatially, some findings challenge this apparent regional coherence: the sole regions with coherent summer warming are found at relatively high latitudes, for winter ice covered lakes (O'Reilly *et al.*, 2015). The systems located in these regions are typically small lakes (Downing *et al.*, 2006). O'Reilly *et al.* (2015) do not include lake size in their clustering. One could wonder whether this could increase the predictive potential of lake surface warming.

Predicting ecological responses are probably tied to even more parameters, as great variability of responses are observed. Herein, our goals were to diagnose the ecological vulnerability of lakes to climate warming and then to explain this variability. Shall the physical vulnerability to climate be important to explain the ecological vulnerability to climate, then the main driver should be linked to some lake geomorphological parameter. If lake morphology is not the only explanatory variable, we hypothesised that local human impact (i.e. TP) could play a role in driving lakes ecological vulnerability to climate change.

### 6.5.2 | METHODOLOGY

Diagnosis of ecological vulnerability to climate warming is often qualitative in lakes (e.g. presence/absence of cyanobacteria blooms). Taranu *et al.* (2015) carried out a quantitative assessment of cyanobacteria dominance on >100 lakes. They demonstrated that most trends were monotonic, which justified the use of Mann-Kendal trend test. Cyanobacteria dynamics are indeed largely driven by nutrient status and the trajectory can relatively easily be qualified (eutrophication, no changes, restoration, Taranu *et al.*, 2015). However, to unpin the variability due to climate, we may not strictly expect a monotonic trend. A more flexible method is needed to account for eventual cross-signals (simultaneous reoligotrophication and response to climate warming). It is with this idea in mind that we turned to multivariate methods to summarise the variability present in the initial data, and then used GAM to quantify the proportion of changes due to climate warming.

The period chosen to model the vulnerability to climate can influence the results (Bruel *et al.*, Under Review). As a result, comparing quantitatively the vulnerability to climate warming of several lakes was an important challenge to address in the first place. One of our objectives was to provide an objective way of quantifying climate driven response in lakes. Herein, we chose Cladocera as the main proxy for ecological state, but the strategy developed could be applied to any other group. Yet, diatoms and pigments that are two classical palaeo-proxies are strongly driven by eutrophication (Taranu *et al.*, 2015), which further increase the risks of detecting changes due to nutrient enrichment in place of climate-driven changes (false positive). Cladocera, by their central position in lake foodweb, are not only impacted by bottom-up change in resources, but also by lateral alterations in habitat structure and top-down impact of predation (Davidson *et al.*, 2011). They are present both in pelagic and littoral habitats (Hann, 1989), and living communities and their sedimentary remains are shaped in broadly similar ways (Davidson *et al.*, 2007; Alric & Perga, 2011). Distinction between specialist and ubiquitous taxa gives an indication on environmental quality. At least in peri-alpine lakes where we are testing our hypothesis, cladoceran communities showed earlier responses to drivers than other planktonic groups (e.g. Alric *et al.*, 2013). Those different factors drove our choice to focus on Cladocera to reproduce ecological state. As the vulnerability to climate has been observed by a change in the assemblage in previous studies (Alric *et al.*, 2013; Milan *et al.*, 2017), we assessed how much variability in the cladoceran dataset could be explained by climate variability.

We are not the first one to attempt a comparison of lake responses to climate change (e.g. Gallina *et al.*, 2013). In here, we are bringing an insight on a longer period, and for more lakes. Yet, our data suffers from irregular sampling and inexistent intra-annual resolution. As a result, there was less than 20 points between 1900 and 2010 in some cases. The interpolation process is mandatory to account for this flaw in the initial data. This step does not compromise the conclusions as the main changes as depicted through ordination axes were perfectly reproduced.

### 6.5.3 | LAKES ECOLOGICAL VULNERABILITY TO CLIMATE WARMING

Our analysis supports the importance of including TP in the analysis and not blindly selecting the dimension with the highest score. However, by including the likely most important drivers of lakes planktonic assemblages (i.e. eutrophication and climate warming, Moss *et al.*, 2011; Bennion *et al.*, 2015b a), we found that most variability explained by climate was found on PC2. The fact that the relationship between residual MAAT and PC2 worked so well supports that climate is an important driver of lake communities. This specific ranking of drivers is further supported by contemporary studies in heavily eutrophicated lakes, where zooplanktonic assemblages are primarily driven by TP (PC1) and then climate (PC2) (Gyllström *et al.*, 2005).

The recent levels of TP explained 50% of the difference in vulnerability to climate warming. Recent assemblages as depicted on axis 2 (Figure 6.8) were characterised by pelagic taxa, both grazers (*Eubosmina* sp.) and predator (*Leptodora kindtii)*. Chronologically, the assemblages were modified in the second part of the 20th century. Eutrophication impacted the littoral area and promoted pelagic taxa as reflected by the contrasted assemblages on axis 1 (Figure 6.8). Negative loadings (periods different from the 1960-1980 period according to our filtering) were indeed associated with littoral taxa, both macrophyte (*Acroperus harpae*) and sediment (*Alona affinis*) associated.

By reducing horizontal diversity, local human impact may have increased the vulnerability to climate change. TP appears as a main modulator of lakes ecological responses to climate change. At the scale of our analysis, we cannot provide a sure picture of the reasons for that, but the identification of the main species characterising assemblages on PC1 and PC2 (Figure 6.8) gives some clues. We transformed the PC1 ordination axes in such way that the periods with the most intense eutrophication would score positive. Conversely, the periods most different in assemblage obtained negative score on PC2. Species loadings were then extracted, and show that negative scores are associated with a somehow high diversity of species, including littoral taxa.

Eutrophication is known to impact littoral areas in shallow lakes, by increasing productivity and triggering the loss of the macrophytic habitat (Scheffer *et al.*, 1993). The limited zones that can sustain macrophytes in deep lakes do not necessarily suppress this mechanism in larger system. A model showed that macrophytes were playing an important role in reducing up to 50% of phytoplankton biomass even deep (100 m), oligotrophic lakes (Hilt *et al.*, 2011).

Our findings should be tested on a larger set of lakes to really strengthen our conclusions. They could realistically be extended to other alpine lakes because they provide a similar good archiving. Limitations include too short records (see Lakes Como and Maggiore that we ruled out to avoid differential time periods), and low confidence in dating.

### 6.5.4 | CONSEQUENCES FOR ADAPTIVE MANAGEMENT

Understanding the responses of systems to climate change is important to predict the impacts of future climatic scenarios (González, Paz & Ferro, 2014; Mina *et al.*, 2017). There are two possible approaches: focussing on one specie or assemblage and look at the shifts in distribution (e.g. Boisvert-Marsh, Périé & de Blois, 2014), our focusing on one ecosystem and study how it respond (our study). In fact, both approaches are tied together, as one ecosystem will directly respond to climate but will also be impacted by potential new stresses (e.g. spread of pine processionary moth with climate change, Tiberi *et al.*, 2015).

While climate is undeniably an important driver of ecosystems, it remains very difficult to predict its exact impacts. On one hand, many studies concur in proving the imprint of climate change on communities composition (Parmesan & Yohe, 2003; Gibson-Reinemer & Rahel, 2015). On the other hand, these responses are not necessarily expressed by the same species being favoured across similar systems (Gibson-Reinemer & Rahel, 2015). In other words, species' range shift are highly asynchronous across areas but the predictability is high at the community assemblage (Gibson-Reinemer & Rahel, 2015).

In large peri-alpine lakes, we could on the overall find a response to climate shared by half of the systems, with pelagic grazers *Eubosmina* sp. and/or predator *L. kindti* benefiting from the new conditions. This linearization of the trophic structure through loss of connection with a diverse littoral zone along with the apparition of a new predator is observed in Lake Geneva (Bruel *et al.*, Under Review).

The climate in our region of study is characterized by warm winters, low air temperature trends in summer, high trends in shortwave radiation in winter, and an increase in shortwave radiation in summer (O'Reilly *et al.*, 2015). Theories state that climate is mostly limiting in cold-environment, while inter-specific relations shape communities in warm-environments (Lenoir *et al.*, 2010). It is possible that lakes that exhibit stronger warming display higher sensitivity to climate, perhaps more decoupled from TP levels at low eutrophication levels.

As we do not observe any threshold of vulnerability linked to geomorphological parameters, it is relatively likely that lakes resistant to current climate warming will also remain more resistant in the future. Those systems seem characterized by lower TP levels, which should encourage managers to pursue their restoration effort as a tool to prevent vulnerability to future climatic scenarios.

Our analysis cannot answer with certitude whether some lakes recover more rapidly than others. Dor instance, Lake Lugano shows relatively low vulnerability to MAAT compared to its eutrophication history. Its large littoral zone may favour its recovery potential, or alternatively, its important relative depth makes it more resilient to climate warming (lesser exposure).

## 6.6 | CONCLUSION

Local human impacts are the most important drivers of lakes ecological trajectory in the Anthropocene. Ambitious restorations programs led to positive results in many systems (e.g. Gulati & Van Donk, 2002; Hilt *et al.*, 2006; Jacquet *et al.*, 2014). However, climate is changing rapidly and may create a new stress on ecosystems worldwide. Deciphering the impacts of climate change from more locally manageable driver has been the purpose of numerous research. Then, while responses are being measured at every organisation level (Scheffers *et al.*, 2016), they may vary greatly from one ecosystem to the other (e.g. in lakes, Livingstone *et al.*, 2010).

We found that local human impact, on top of being an important driver of ecosystems, is also most-likely driving lake ecological vulnerability to climate change. Under the hypothesis that ecosystems resistance to climate variability was disrupted by local human impacts (Bruel *et al.*, Under Review), this only suggest that ecosystems that were impacted in a greater extent are now more vulnerable to climate warming. Interestingly, the relationship appears relatively decoupled from exposure to climate warming as we did not find a correlation between rate of warming and vulnerability to climate warming for this set of peri-alpine lakes.

Our analysis does not say whether or not this vulnerability to climate warming will eventually fade away as the recovery debt will pay itself (Moreno-Mateos *et al.*, 2017). Adaptive management strategies could include the restoration of littoral zone, which were largely impacted by eutrophication (in Lake Lugano, Ravera & Parise, 1978; in Lake Varese, Bruel *et al.*, 2018).

Our study confirmed that long-term perspective is valuable to understand lakes ecological trajectory under multiple stressors, especially when assessing the impacts of non-stationary variables such as climate change.

## 6.7 | ACKNOWLEDGEMENT

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# Chapter | 7

# Discussion and perspectives

# 7 | DISCUSSION AND PERSPECTIVES

The organisation of Earth systems is shaped by a number of geologic and climatic parameters acting across enormous ranges of scales, together with inter- and intraspecific interactions (Levin, 1992). In short, ecosystems are the complex output of both space and time constraints (Wolkovich *et al.*, 2014). The identification of these forcings as well as the understanding of the mechanisms at work enable to draw theories on systems functioning (Leavitt *et al.*, 2009). At the global scale, climate is probably one of the parameter with the most intuitive consequences on system organisations as temperature, solar radiance, humidity, precipitations, and wind variability determine tropical, temperate or artic environments. Besides those abiotic factors, inter- and intraspecific interactions also shape the ecosystems through competition, predation and cooperation, reducing the fundamental niche to the realised niche (Figure 7.1). Under these specific constraints, species evolve or disappear (Darwin, 1859). Finally, the structure of ecosystems is defined by colonisation, extinction, and isolations patterns (Baldi, 2003). Space and time constraints give rise to endemism, the state in which specie is unique to a specific geographic area. For instance, continental drift lead to higher speciation than what a well-mixed system would have sustained (Jordan, Barraclough & Rosindell, 2016). To summarize, 'the variability of species in a state of nature […] can be treated properly only by giving long catalogues of facts' (Darwin, 1859).

Human influence disrupted the natural pattern of evolution for the past millennia. Introducing species to isolated land has the potential to drive extinct native species that cannot compete with predator-free new arriving (Lodge, 1993). In an absolute sense, and since human started impacting its environment at a greater scale, land use override climate change in term of quantity of changes brought to ecosystems trajectories (Parmesan & Yohe, 2003). However, the fact that consequences of climate change are measured worldwide at every level of organisation forbid ruling out the threat (Scheffers *et al.*, 2016). Moreover, local drivers are more easily managed than global ones (Rocha, Peterson & Biggs, 2015).

Our objective was to evaluate the ways local and global stressors interact in driving peri-alpine lakes ecological trajectory, and then to understand whether local human impact decreased the systems resistance to climate warming. In this section, I go over the main outputs of our work and their implication. Then, I discuss some of the limitations of our approach. Finally, I summarise the major analytical outputs developed in the framework of my PhD, and go over potential research directions and perspectives.

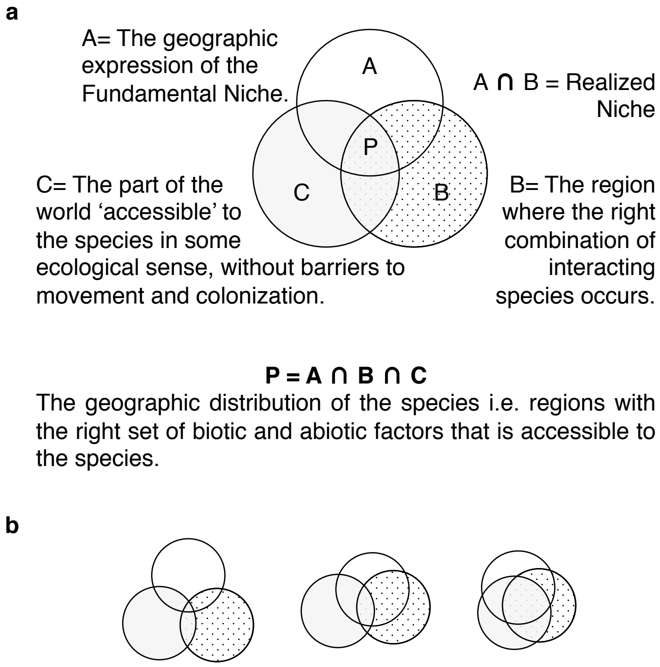


**Figure 7.1** I Concept of fundamental and realised niches.

(a) Geographical distribution of species depends on their Fundamental Niche i.e. the part of the world with adequate abiotic drivers (A). Species distribution also depends on biotic factors (B). A ∩ B is the realized Niche. A ∩ B ∩ C is the actual distribution of the species, also modulated by (C), the part of the world 'accessible'. Redrawn from Soberon & Peterson (2005). (b) A, B and C overlaps can be more or less important, and can vary with time.

## 7.1 | Lakes vulnerability to climate change in a human-driven planet

The co-occurrence of multiple stressors on a given ecosystem is the norm rather than an exception (e.g. Schäfer *et al.*, 2016; Wu *et al.*, 2018), and many studies are investigating the potential interactions between drivers (i.e. additism, antagonism, and synergism, Darling & Côté, 2008; Chui & Ang, 2017). Our overall questions were to (1) understand whether lakes ecological vulnerability to climate change were impacted by degree of local human impacts, and if so, (2) how much?

### 7.1.1 | Multi-stressors

Lake Varese (North Italy) underwent drastic restructuration over the course of the 20th century. The system is now on a restoration pathway, but appears to resist any further decrease in nutrient concentrations. Several stressors, both local (total phosphorus, TP) and global (mean annual air temperature, MAAT), are successively driving its pelagic assemblage (see **Chapter 4**). At the scale of the past 170 years, the assemblage underwent three transitions, one of which was linear and the others abrupt. The first abrupt transition followed the dramatic increase in TP (from <25 µg P.L$^{-1}$ to >100 µg P.L$^{-1}$). *Daphnia* spp. was replaced by the grazer *Eubosmina* sp.

and the opportunist *Chydorus sphaericus* (Figure 7.2). From the 1980s, a new wastewater treatment plant allowed the limitation of nutrient fluxes to the lake, resulting in a partial decrease of in-lake TP, but it is climate warming that is now controlling the pelagic cladoceran assemblage of Lake Varese.

**Local and global stressors can successively impact ecological assemblages** (Alric *et al.*, 2013; Bruel *et al.*, 2018)**. In a changing climate, results from ecological management actions may be buffered by the presence of new forcings. It is important to document the interactions among stressors to understand the reasons for little results in order to avoid a crisis of motivation among managers** (Mumby *et al.*, 2017)**.**

### 7.1.2 | FRESHWATER ECOSYSTEMS THREATS

In **Chapter 5**, we worked on a long record covering the past 1,250 years, and highlighted that all the ecological transitions the lake underwent took place over the past century. The main one was the 1961 / 1963 transitions that saw a shift between the initial assemblage composed of the post-glacial colonizer *Eubosmina logispina* and macrophyte-associated *Sida crystallina* toward an assemblage dominated by *Daphnia* spp. The quantification of principal drivers led to the conclusion that eutrophication drove most changes in the cladoceran assemblage at the scale of the past millennium.

**This long-term recoil supports the idea that local human impact is currently the main threat for biological communities** (Parmesan & Yohe, 2003)**. In many cases, in Europe at least, lake managers were able to achieve restoration from eutrophication because they had hands on the driver** (Hilt *et al.*, 2006; Jeppesen *et al.*, 2007; Jacquet *et al.*, 2014)**. Managing ecosystems in face of climate change requires a different approach** (e.g. building ecosystem resilience, Epple & Dunning, 2014) **as tackling climate warming requires a global consensus.**

### 7.1.3 | MODULATION OF VULNERABILITY TO CLIMATE CHANGE BY LOCAL STRESSORS – TEMPORAL APPROACH

Is resistance to climate variability is a stable property of ecosystems? While the main driver of Lake Geneva ecological trajectory over the last millennium is indubitably eutrophication (**Chapter 5**), we could find the imprints of climate warming already documented by a previous study (Alric *et al.*, 2013) on the cladoceran assemblage. General additive models (GAM) could not model the relationship when the whole record was considered. Indeed, GAM is not designed for situation with bistability i.e. different levels of vulnerability for a same level of stress. We thus cut the dataset into two time periods, before and from the beginning of the local human impacts. Regardless of the window used to model ecological responses versus climate on axis 2, we did not evidence a vulnerability to climate warming before the 20th century. However, the recent assemblage is responding to climate warming (Figure 7.3).

**We concluded that Lake Geneva has entered a new vulnerability regime in the 20th century, following its fundamental alteration by local human activities. Restoration does not guarantee a return of the initial functioning** (Moreno-Mateos *et al.*, 2017)**.**

### 7.1.4 | MODULATION OF VULNERABILITY TO CLIMATE CHANGE BY LOCAL STRESSORS – SPATIAL APPROACH

Is climate ecological vulnerability a function of exposure to climate change, or is it derived from previous history of perturbation? Results from Lake Geneva (**Chapter 5**) underline the impact of local drivers on resistance properties of lakes to climate change. Lakes display different levels of response to climate change (Livingstone & Padisák, 2007; Perga *et al.*, 2015). In **Chapter 6**, we questioned whether we could identify the factors making some lakes more ecologically vulnerable than others.

Three main hypotheses were that ecological vulnerability to climate warming depended on (1) climate exposure, (2) local human impacts, or (3) the combination of both parameters. In the first scenario, local human impacts would act as a switch between the resistant and vulnerable regimes (**Chapter 5**), and further vulnerability to climate warming would be mediated by geomorphological parameters (maximum or mean depth, surface area). In the second scenario, the resistance would not be a binary system property (present/absent) but rather a capital that can be spent. Consequently, the resistance of systems would depend on the intensity (extent and/or cumulative) of previous perturbations. Rather than a capital, the resistance may be the sum of ecosystems functions/properties e.g. presence of the littoral zone, good benthic oxygenation. The final scenario would consider that both these aspects are determining lake ecological vulnerability to climate warming.

We found that the vulnerability to MAAT was best explained by average TP concentrations over the past 20-years. The relationship is most likely non-linear, although it is difficult to fit with certitude a relationship based on the number of lakes we worked on. Non-linearity of the relationship linking the vulnerability to climate vs. local human impact is likely due to the fact that beyond a certain level of eutrophication, MAAT cannot be the only driver of the trajectory.

More records should be added to our analysis to confirm or challenge our conclusions. TP may not be available for every lake, but working on the 2nd principal component (PC2, and making the assumption that PC1 is explaining responses to TP gradient) appears reasonable based on our subset. This assumption may only be true for lakes with a similar history of eutrophication i.e. at the scale of the past century.

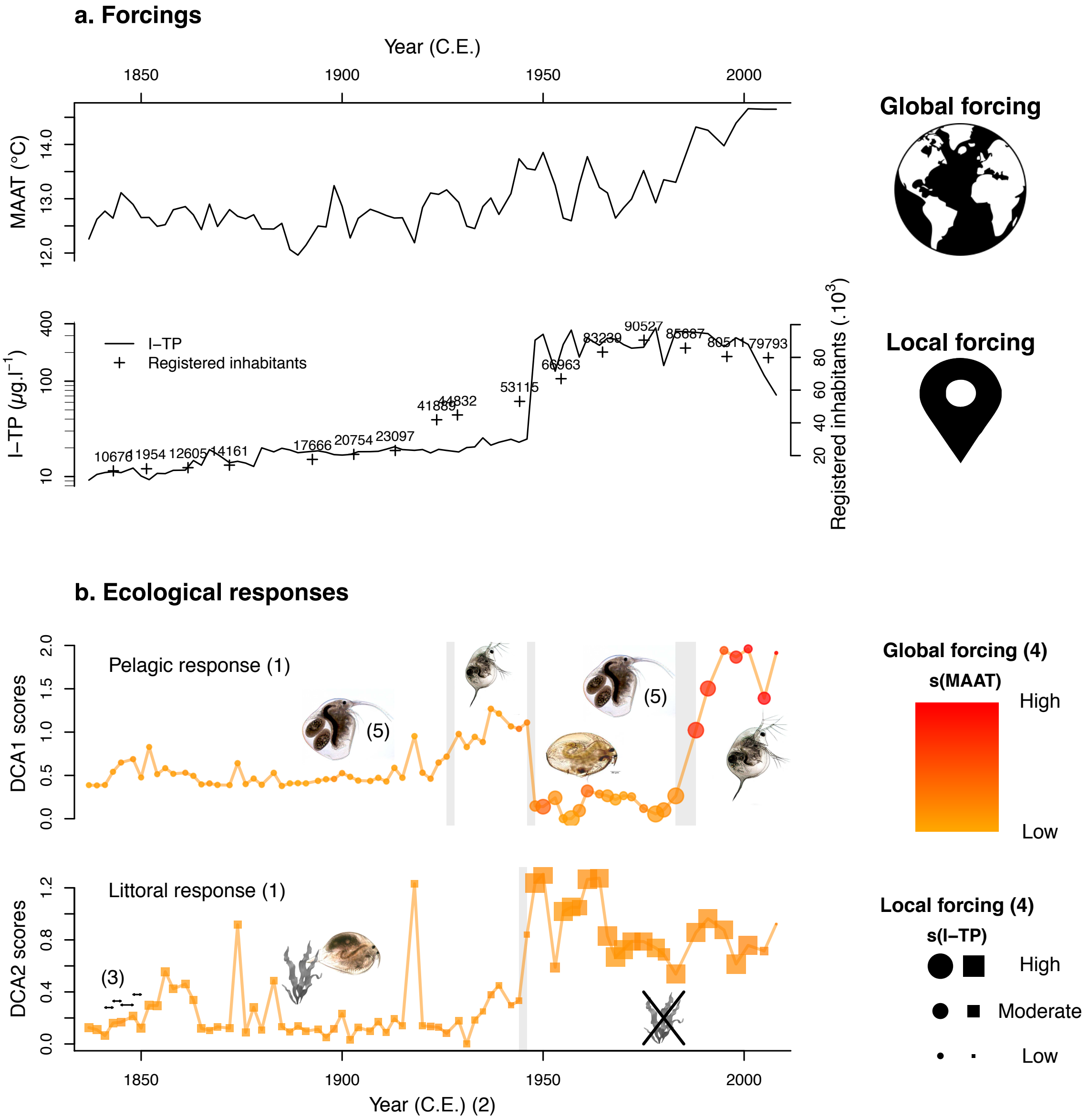
As far as we know, it is the first time that an assessment of ecological response to climate is carried on across systems. It is difficult to do so because eutrophication is often the dominant driver in freshwater systems. Many study are carried out on algae and their response to eutrophication (e.g. Taranu *et al.*, 2015; Monchamp *et al.*, 2017), because the bottom-up effect is well documented. Consequently, strong hypotheses have to be made to unpin the effect of climate change: (1) the climatic gradient is depicted on PC2 and (2) linear interpolation does not affect the data. Principal component analysis (PCA) is an ordination method designed to identify main gradients in floristic and faunistic lists, and across our lake subset, it ranked TP as the main driver of cladoceran dynamics (Gyllström *et al.*, 2005). The interpolation step was important to confer the same weight to the different periods, and did not impact the PCA , as tested comparing raw vs. interpolated data (**Chapter 3**).

**Peri-alpine lakes vulnerability to climate change appears linked to the local history of eutrophication. While it is probably not the only parameter modulating the responses to climate warming, it may have reduced the lakes natural resistance to other forcings.**

### 7.1.5 | REGIME SHIFT IN DEEP SYSTEMS

Resistance to restoration in freshwater ecosystems has often been attributed to possible hysteresis mechanisms (reviewed in Hilt, 2015). Alternatively, the changing baseline conditions brought by climate warming may explain delays in restoration (Battarbee *et al.*, 2005). The unambiguous diagnosis of regime shifts (abrupt transitions along with hysteretic responses to main drivers) requires several steps (Andersen *et al.*, 2009). First, abrupt transitions need to be identified, which requires a relevant scale of observation i.e. a long-term vision to decipher natural variability from actual transitions. For instance, some species display well-documented cycles over several decades (e.g. inter-annual fluctuations of herring and sprat in the Baltic Sea, Casini *et al.*, 2006), constrained by fluctuations in top-down control rather than bottom-up pressures. Correct assignment of abrupt vs. linear shift requires a sufficiently high resolution (i.e. close to the life-cycle of the focus group). Secondly, regime shift diagnosis absolutely requires identifying potential drivers (Andersen *et al.*, 2009). Careful selection and open hypotheses about the shape of the relationship can only increase the success of the diagnosis (I discuss further the model aspect below). Finally, the shape of the relationship (response vs. driver) is probably the best argument to show hysteresis (e.g. hysteresis between air and surface water temperatures in deep lakes, Toffolon *et al.*, 2014).

## Chapter 4 – Graphical abstract



Take–home messages:
(1) Spatiality of responses (pelagic vs. littoral)
(2) Long–term insight to decipher between global and local drivers
(3) High–resolution to understand dynamics
(4) Different vulnerability to drivers over time
(5) The same specie can be favored under different conditions

**Figure 7.2** I Key messages from Chapter 4.

(a) Mean annual air temperature (MAAT) and inferred total phosphorus (I-TP, log-scale) were considered as the main drivers of Lake Varese ecological trajectory. They are respectively global and local stressors. The registered inhabitants in the city of Varese are plotted next to I-TP. (b) Ecological responses over the past 170 years in Lake Varese, through the first two dimensions of detrended correspondence analysis (DCA). DCA1 reflects changes in pelagic assemblage, while DCA2 reflects changes at the littoral scale. Colour scale reflects the contribution of MAAT to each period (red means high contribution). Size reflects the contribution of I-TP on the assemblage.

In **Chapter 4**, we propose a workflow analysis aimed to detect regime shift dynamics from palaeo-datasets. Most ecological evaluations are hampered by the lack of observational datasets. In such case, palaeolimnology presents a unique opportunity to investigate long-term ecological dynamics. The limits of the method are mostly tied to the resolution and reconstruction of drivers (discussed).

We did not find evidence for nutrient-driven regime shift in the pelagic assemblage of Lake Varese, which switched at a TP threshold in between 25 and 200 µg TP.L$^{-1}$. As the TP levels are still around the higher threshold (100 µg TP.L$^{-1}$), we cannot conclude to any bistability. Besides, the high contribution of MAAT to the recent assemblage suggests that even if TP levels were significantly reduced, the assemblage would remain driven by climate warming. The littoral assemblage, on the other hand, tipped for a much lower TP threshold (24-25 µg TP.L$^{-1}$). The threshold is also lower than what has been observed in shallow lakes (an excellent model-system for regime shift theories), but consistent with what could be expected in deeper lakes (Capon *et al.*, 2015).

We computed early warning signals (EWS) from the ecological records. EWS cannot be self-diagnosis tools of regime shifts (Burthe *et al.*, 2015), but they offer the possibility to rule out natural variability from potential resilience loss (Spears *et al.*, 2017). EWS (increased variance and autocorrelation) were detected in the littoral assemblage before the 1940s shift. Moreover, those indicators stabilised after the main transition, suggesting a new stable state. Again, since the critical threshold has not been crossed back, we cannot evidence any true hysteresis (i.e. bistability).

**Our findings confirm the importance to consider several stressors when assessing ecosystems trajectory. Global and local drivers can successively or simultaneously drive ecosystems trajectory. Main drivers can be identified with palaeolimnological tools, but a sufficiently high resolution is mandatory to investigate EWS and identify spatial shifts. A loser sampling could have missed the spatiality between the littoral and pelagic shift and would have omitted a part of the story.**

### 7.1.6 | SPATIALITY OF TRANSITIONS IN DEEP LAKES

The spatiality of the dynamics in Lake Varese (**Chapter 4**) was one of the main surprises. In parallel to the main pelagic transitions observed in Lake Varese, the littoral assemblage taught a slightly different story. For starts, only one transition (versus three in the pelagic) was evidenced, between 1944 and 1946 i.e. just before the second one in the pelagic assemblage. Littoral diversity was crushed. This single transition, for TP levels <25 µg TP.L$^{-1}$ according to the transfer function based on pigments analysis (CarI-TP), suggests the littoral area has switched for a really low nutrient threshold. The transition chronology suggests the littoral zone may have played a buffering role for nutrient loads, until it disappeared and the whole lake changed.

In Lake Geneva (**Chapter 5**), assemblages' compositions under the different regimes of vulnerability to climate variability were further scrutinized. Before 1961, the large macrophyte-associated *Sida crystallina* represented continuously ~30 % of the total assemblage (Figure 7.3). During the transient warming period in the 1940s, its relative or absolute abundance further increased. The predator *Leptodora kindtii* thrived in the re-oligotrophication assemblage, and the dominant species are all pelagic taxa. Loss of littoral taxa in the vulnerable state raises the question of its role in the ecological resilience of deep lakes to climate warming. More complex horizontal diversity is typically a factor of resilience, in which taxa are less prone to extinction cascade (Barbier *et al.*, 2018). The new top-down pressures (presence of the predator *L. kindtii*) on grazers species (*Bosmina* sp. and *Daphnia* spp.), as well as climate warming, may stress the ecosystem in a greater extent than it used to when there was a functional littoral zone.

Lake Garda different basins (Brenzone, northern deep basin, and Bardolino, southern shallower basin) displayed different vulnerability to the climatic driver MAAT (**Chapter 6**). It further supports the potential for spatiality of trajectories in large system. The most vulnerable basin (Bardolino) also suffered less from eutrophication over the past few decades (Milan *et al.*, 2017). The basin is located closer to the inflow and present an important depth/surface ratio, which probably increases its resistance to eutrophication.

**The disappearance of the littoral habitat is symptomatic of eutrophication** (Chapters 4-5, Ravera & Parise, 1978). **It is possible that, even in deep lakes, littoral zone play an important role in their resilience to external stressors. The deepest point is typically sampled in large systems** (as for instance SHL2 in Lake Geneva monitored by the hydrology station CARRTEL since 1956)**, but the insights from littoral and benthic zones** (e.g. Rimet, Bouchez & Montuelle, 2015) **to the health of the ecosystems may constitute interesting and relevant research directions.**

## Chapter 5 – Graphical abstract

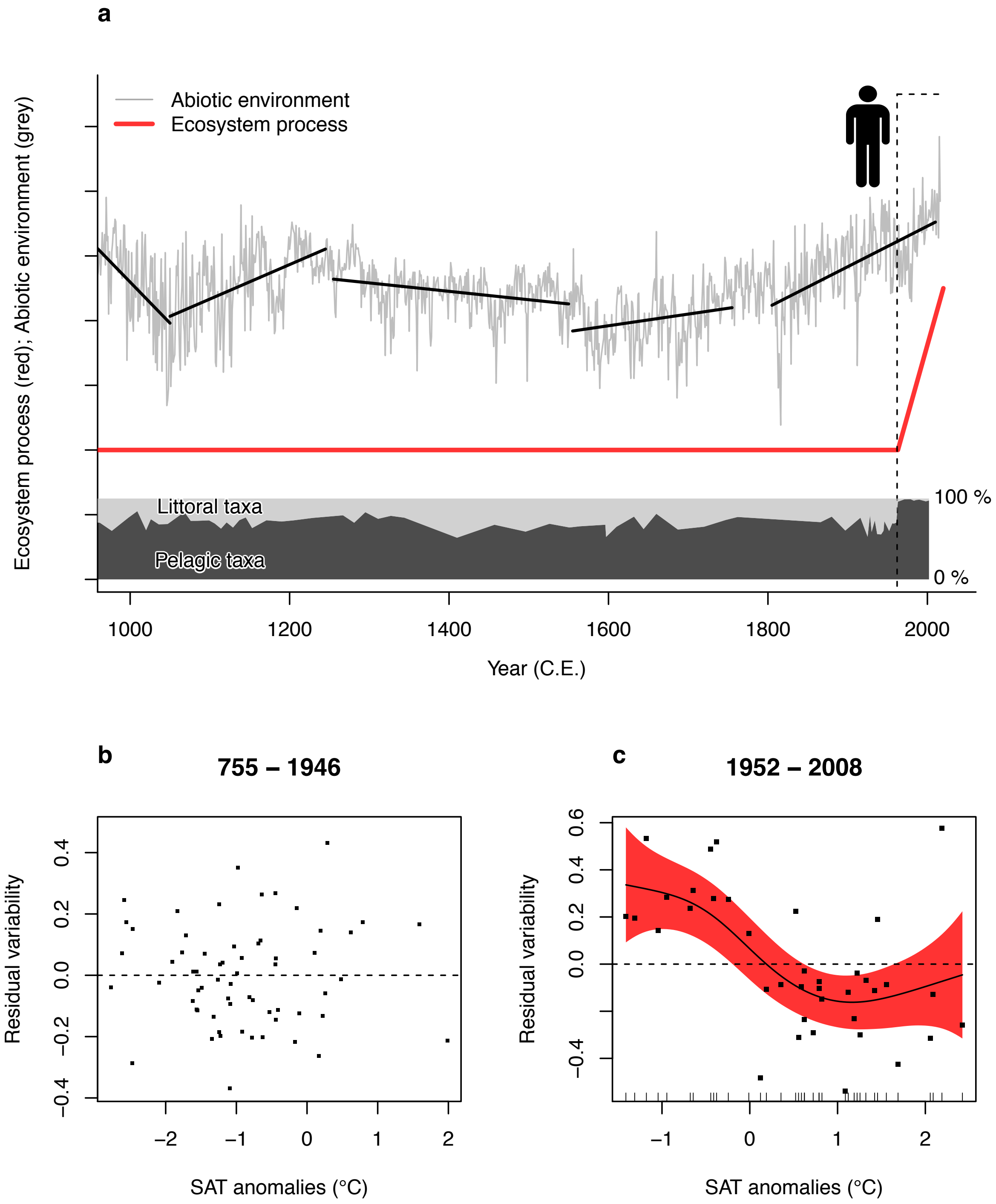


**Figure 7.3 I** Key messages from Chapter 5.

(a) Lake Geneva ecological vulnerability (red) to climate variability. Climate (grey) is a highly non-stationary variable (see trends in black). The proportion of littoral vs. pelagic taxa over the record is shown. (b) Lake Geneva displayed a high resilience until human activities locally impacted the system over the course of the 20th century. Since then, (c) the system display responses (i.e. low resistance) to climate warming.

## Chapter 6 – Graphical abstract

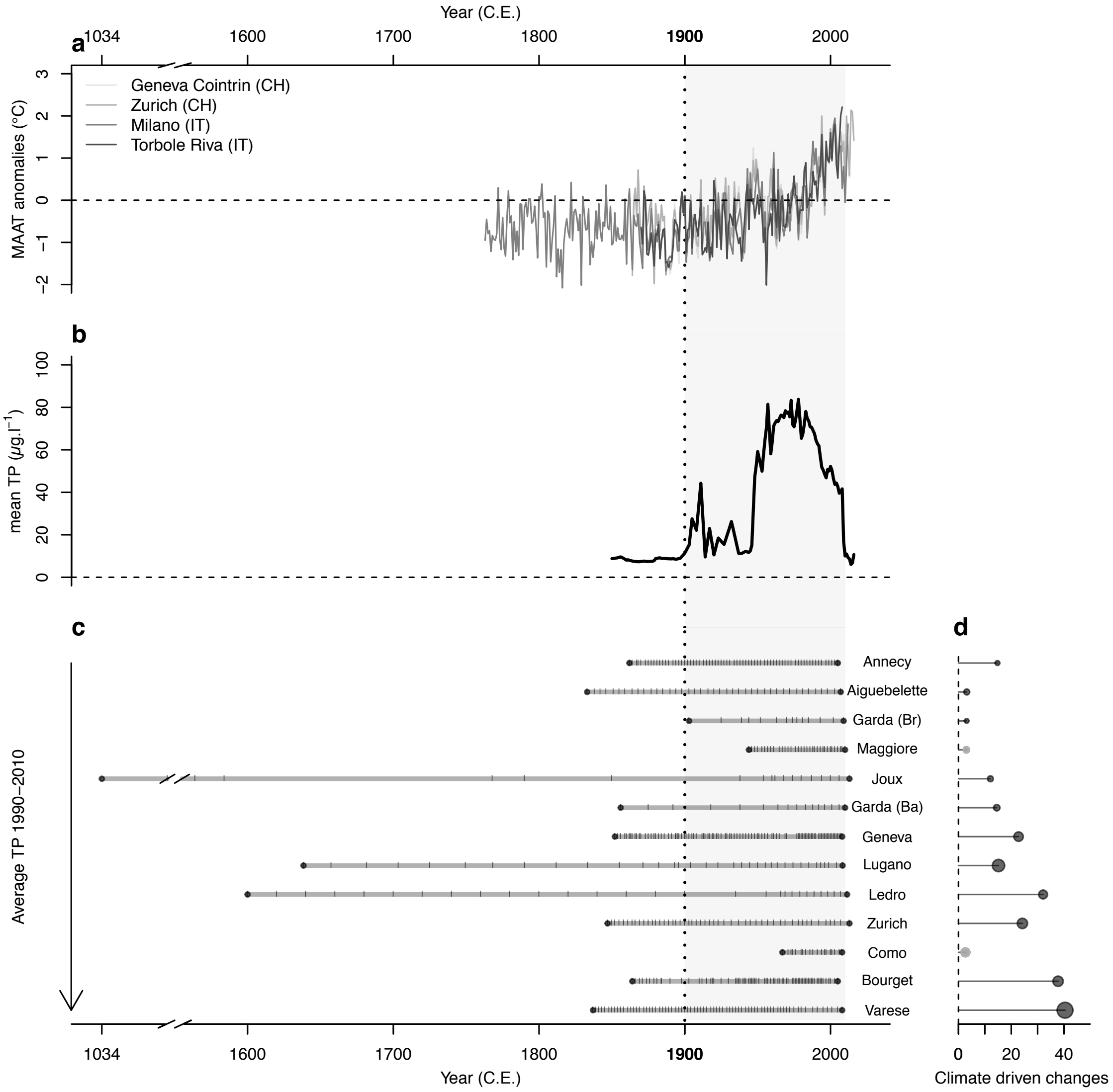


**Figure 7.4 I** Key messages from Chapter 6.

(a) Mean annual air temperatures (MAAT) anomalies for the four weather stations used to account for the climatic forcing. Geneva Cointrin for Lakes Aiguebelette, Annecy, Bourget, Joux, Geneva; Zurich for Lake Zurich; Milano for Lakes Maggiore, Varese, Lugano, Como; Torbole Riva for Lakes Garda and Ledro. (b) Average mean total phosphorus (TP) for the 9 lakes with TP reconstruction data. (c) Period covered by each sediment records. Black dots mark the first and last sample, and small vertical tick marks indicates the location of each sample. Lakes are ordered by increasing average TP over the last 20 years of the focus period (1990-2010), a proxy for local human impact. (d) Climate driven changes in each lake. Size of the dots reflects the maximum level of phosphorus reached in each lakes over the past century. Grey dots represent Lakes Maggiore and Como that were discarded from the analysis because their record did not covered the past century.

## 7.2 | LIMITATIONS OF MY RESEARCH

### 7.2.1 | SAMPLING AND DATING

We based the approach on palaeolimnology tools. The replicate on several lakes confirms the strength of palaeolimnology as a mean to reconstruct past environments. Large peri-lakes display good characteristics for sequential sedimentation, which make them good candidates for high-resolution study (Perga *et al.*, 2015).

High-resolution sampling was an important requirement to investigate ecological theories beyond ecological trajectory reconstruction. For instance, we could confidently trust the EWS in Lake Varese because the total sequence was available. On the other hand, the (by-comparison) low sedimentation rate in Lake Zurich limited the resolution of the study to ~7 years. If we try calculating EWS on a 20-years window like in Lake Varese, we will be using 3 samples, and too little samples has been shown to impact the outcome of the EWS calculation (see **Chapter 3**).

In **Chapter 5**, we reconstructed the long-term ecological trajectory of Lake Geneva, the largest lake of Western Europe, over the past 1,250 years. The ideal context was brought together to investigate our question i.e. (1) a well constrained sediment record (Kremer, Simpson & Girardclos, 2012), (2) a good sequential sedimentation allowing annual sampling in the upper core (Alric *et al.*, 2013), (3) a local reconstruction of climatic data (Büntgen *et al.*, 2006), and (4) long-term monitoring data to avoid uncertainties linked to high-resolution sampling (SI OLA, Thonon-les-bains).

Although the biological records (both cladoceran and diatoms) were stable until the 20th century, the high-resolution was mandatory to correlate the responses with the climatic data. Short-lived radionuclides can only date the past century, and radiocarbon ages come with great age uncertainties. The long sediment record in Lake Geneva was luckily really well constrained by a documented tsunami deposit in 563 AD (Kremer *et al.*, 2012) and the coring year, while the recent-most part was dated resorting to radionuclides measurement. Palaeomagnetic inclination and declination fields were measured on the rest of the sequence, which allow a good correlation to reference curve and narrowing the age uncertainties.

**The assets of the long-term study on Lake Geneva (Chapter 5) rely greatly on the high-resolution dating we were able to build and the well-known context of the system. The sedimentation of lakes and the possibility to carry out high-resolution sampling would be the main limitation if we were to extend the results from Chapters 4 and 6 to other systems.**

### 7.2.2 | CLADOCERA AS PROXY OF ECOLOGICAL CHANGES

We focussed the quantification of ecological vulnerability on one group, Cladocera. It would be interesting to confront our results to results obtained through other proxies on many lakes. Yet, a syntheses of studies carried out on Lakes Annecy, Bourget and Geneva for several proxies (Perga *et al.*, 2015) shows consistent shifts across groups. Similarly, shifts in diatoms and chironomids assemblages were consistent in three Chinese lakes (data compiled in Doncaster *et al.*, 2016). Same conclusions are reached by a new study currently carried out on Lake Joux, with the objective to compare the information brought by several proxies (cladoceran, chironomid and fish remains, phytoplankton pigments, DNA-based methods, see abstract in Appendix). Besides, a focus on primary producer group would increase the contribution of eutrophication to the deviance explained.

**Cladocera, for their central position in the food-web, their high sensibility to both top-down and bottom-up processes, their littoral and pelagic distribution, and their easiness of identification, constitute a good focal group. Furthermore, unlike pigments and DNA-analysis, no specific conservation of the sediment is required to analyse cladoceran remains, which allow working on sampled cores, reducing the cost of any extensive study. The main cost concerns the operator time.**

### 7.2.3 | RECONSTRUCTION OF DRIVING FORCES

Herein, and following previous findings (Perga *et al.*, 2015), we made the strong hypothesis that TP and MAAT would explain most of the trajectory of deep peri-alpine lakes.

Not having direct nutrient loads is clearly a limitation, and multi-indicators studies are highly valuable in this respect (e.g. Bunting *et al.*, 2016). However, TP reconstruction through diatoms assemblage allows grasping a large part of the eutrophication dynamics, which are known to be important drivers of freshwater ecosystems. Diatom-inferred TP (DI-TP) is a much used proxy to infer past levels of TP (Lotter *et al.*, 1998; Marchetto *et al.*, 2004; Battarbee, 2005). However, they appear to resist early increase in TP, as suggested by the different timing of modifications in pigments and diatom assemblages observed in Lake Varese (**Chapter 4**). Furthermore, they may display a lag between restoration and responses to lower TP (Berthon *et al.*, 2013). Direct nutrient loads would constitute a better proxy for local human impact, but such data are difficult to obtain for long-time period (Wang *et al.*, 2012). In **Chapters 4** and **5**, we built composite TP between pigments and diatoms transfer function (Lake Varese), and diatoms transfer function and monitoring data (Lake Geneva). Our objective in both cases was to get the closest possible picture of the real eutrophication history. We highly encourage others to do the same when confronted to similar choices.

If efforts can be made to integrate other drivers, they should focus on integrating fish predation pressure, that can present a great top-down control on cladoceran communities (Vanni, Layne & Arnott, 1997; Feniova *et al.*, 2015). Quantification of predation pressure was done for Lakes Annecy, Leman, and Bourget, but was found to be impacting cladoceran structure only in the former system (Perga *et al.*, 2010; Alric *et al.*, 2013).

**Palaeolimnology is classically based on a space for time substitution approach, with the assumption that drivers shaping biological communities in contemporary study were also shaping the same species centuries ago** (Hann, 1989)**. As such, Cladocera communities are mainly shaped by nutrient levels and climate** (Gyllström *et al.*, 2005)**. Fish predation is also an important driver of zooplankton assemblage, and should be included when accurate reconstructions are possible.**

### 7.2.4 | INTERACTING STRESSORS

Another aspect that we did not explore in depth but is worth mentioning is that interacting forcing may diminish our capability of predicting regime shifts from EWS (Brock & Carpenter, 2010). It can affect easily computable metrics such as variance, as we did in **Chapter 4**. Indeed, parallel forcing(s) may independently generate variance in the state variable used to anticipate shift (in our case, we are using cladoceran community composition). If this variance is greater than the variance generated by the forcing that can cause the system to shift (see **Chapters 2–4** for details on early warning signals), then the variance may be muffled and one could miss the early warning (Brock & Carpenter, 2010). Conversely, if the variance in isolation is smaller than the variance due to the forcing that may cause the ecosystem to shift, then the overall variance can be magnified (Brock & Carpenter, 2010).

In such cases, long-term perspective can help distinguished natural variance from the one of a system approaching a shift (Spears *et al.*, 2017). In **Chapter 4**, we do not explore the potential interaction between variance due to the non-stationary forcing i.e. climate and variance due to the stationary forcing that may have caused a regime shift in Lake Varese i.e. eutrophication. Yet, we only found signs of early warning signals for a system approaching a regime shift on axis 2, which is the axis where eutrophication was the only significant driver. The impacts of climate on axis 1 may have muffled the early warnings signals, which would explain the monotonic increase in variance generated from the scores on this axis.

### 7.2.5 | MODELS IN MODERN ECOLOGY

Typically, models must impose hypothetical constraints to give useful estimates, or they will suffer from the general unbalance between number of unknowns and number of observations (Schnute & Richards, 2001). Consequently, when we investigated the relationship between climate and ecological responses at the scale of the past 1,250 years, the fact that we did not find any relationship was suspicious. Indeed, Lake Geneva ecological communities have been shown to respond to climate in studies using monitoring (Anneville, Gammeter & Straile, 2005; Anneville *et al.*, 2009) and palaeolimnological data (Alric *et al.*, 2013). We then formulated the hypothesis that ecological vulnerability may have changed over the course of the past century. Repeating the analysis assuming a change in vulnerability allowed us to reproduce the results of Alric *et al.* (2013), and evidence a long-term resistance of Lake Geneva to climate variability before ca. 1946.

In line with previous findings (Schnute & Richards, 2001; Giron-Nava *et al.*, 2017), we conclude that models often underestimate non-linearity. Including many drivers in the pre-analysis is another strategy for exhaustivity (e.g. Bunting *et al.*, 2016). However, more parameters do not drastically increase the understanding of the shifts, as especially in lakes, eutrophication, climate, and change in predation pressure appears to be the most important drivers of systems trajectory. Indeed, a literature review concedes that most patterns documented in natural systems are remarkably simple, in defiance of the potential complexity of biotic changes (Parmesan & Yohe, 2003). Specie-oriented studies have low chances of replicates (Gibson-Reinemer & Rahel, 2015), but changes at the assemblage scale are surprisingly consistent (Parmesan & Yohe, 2003; Gibson-Reinemer & Rahel, 2015).

**The field of Ecology needs to acknowledge and embrace that non-linearity of responses is rather the norm** (Milly *et al.*, 2008)**. Consequently, models calibrated for the past 20 years may not necessarily extrapolate well in the future. For instance, Mina *et al.*** (2017) **predicts the shift in forest distribution and offer management recommendation, but do not include potential supplementary drivers such as parasites that could spread with new temperatures.**

## 7.3 | ANALYTIC OUTPUTS OF THE PHD

Four reproducible methods were elaborated as part of this PhD, allowing to (1) build age-depth models from radionuclides measurements, (2) detect regime shifts, (3) assess potential bistability to a given driver, (4) quantify the ecological vulnerability to climate across systems.

### 7.3.1 | SHORT-LIVED RADIONUCLIDES AGE MODELLING OF RECENT SEDIMENT CORES

Short-lived radionuclides are measured in surface sediment to provide geochronology over the past century. The different steps require a certain expertise and understanding of lake sedimentation. A R code was produced to semi-automatically build the age-depth models presented in **Chapter 2**. It allows simple computation and comparison of different $^{210}Pb_{ex}$ model (CFCS, CIC, CRS) and sedimentation hypotheses (change in sedimentation rates, instantaneous deposits, slumps, etc.). The code will then be published to be accessible to the scientific community (see Appendix for abstract).

### 7.3.2 | REGIME SHIFT DETECTION FROM PALAEO-DATASETS

Ecosystem resistance to restoration is often attributed to potential regime shift dynamics without providing a critical appraisal of the evidences (see Capon *et al.*, 2015 for review on the matter). As long-term datasets are required to rule out natural variability from unstable system (Spears *et al.*, 2017), we tested whether we could detect signs of regime shift from palaeo-records. **Chapter 4** provides an application of this method to the ecological trajectory of Lake Varese.

### 7.3.3 | TESTING BI-STABILITY OF RESPONSES

In ecology, stressor-effect relationship are often represented as linear or sigmoidal relationships (Schäfer & Piggott, 2018). In parallel, research on the impacts of multi-stressors acknowledge the complexity of interactions (see Chapter 1 and Piggott, Townsend & Matthaei, 2015). In **Chapter 5**, we hypothesised that history of perturbation may modify the ecosystem vulnerability to a given stressor. In other words, there would be a 'temporal synergism effect'. This hypothesis is backed up by the quantification of a recovery debt (i.e. a period during which ecosystem functions are not recovered despite restoration, Moreno-Mateos *et al.*, 2017) in various ecosystems. More details on the method are given in **Chapter 3**. Based on our findings, it is possible that more systems show such bi-vulnerability; it would be useful to produce a model that account for this hypothesis.

### 7.3.4 | VULNERABILITY TO CLIMATE CHANGE ACROSS SYSTEMS

The first difficulty to overcome was to hierarchize vulnerability across systems. We wanted a method that would work even for non-monotonic trend i.e. appearance/disappearance. Furthermore, we anticipated that local human impacts would be driving most of the changes in the assemblage, as we purposely selected a set of lakes that followed a large eutrophication gradient.

In **Chapter 6**, we homogenised the dataset by working solely on the 1900-2010 period, and interpolated the data to get a yearly resolution. We then converted the multivariate dataset into ordination axes resorting to principal component analysis. At this step, we compared the PCA computed from raw data and the PCA computed on interpolated dataset and confirmed the dynamics were well reproduced. For the lakes with both TP and MAAT available, we ran GAM using the three combinations of drivers (i.e. TP, MAAT, TP+MAAT). We found a good correlation between the overall residual variance explained by MAAT when the most exhaustive model was used (TP+MAAT) and the variance explained by MAAT on PC2. TP is driving most of the ecological trajectory in peri-alpine lakes (Gallina *et al.*, 2013; Monchamp *et al.*, 2017). Hence, the first gradient at the scale of the past century was found on PC1. Subsequently, the changes driven by climate warming were carried by PC2, similarly to the observation made in **Chapter 5**.

### 7.3.5 | PERSPECTIVES: RESILIENCE MECHANISMS IN DEEP LAKES

The long-term approach reveals both Lakes Varese and Geneva littoral zones were impacted by eutrophication. The impact was revealed by the loss of macrophyte-associated species. Lakes Varese and Geneva are respectively the smallest and largest systems of our study, and both shifted for inferred-TP below 25 µg TP.L$^{-1}$. The key role of environmental interfaces is established in various environments (e.g. riparian zone, Hancock, Ladd & Froend, 1996). Lakes littoral zone alteration by local human impacts constitutes a possible mechanism by which resilience was lost.

Interfaces are generally characterized by harsher conditions than the environments they delimit. It also favours more diversity following the intermediate disturbance hypothesis that predicts a hump-shaped pattern between community diversity and disturbance. For instance, lakes littoral zone is thermally less stable than the pelagic zone (Yamanaka *et al.*, 2012). Cladocera present higher littoral than pelagic diversity (Bjerring *et al.*, 2009): littoral habitat include macrophytes and sediment substrates, while pelagic zone is characterized by open waters.

The cores we worked on were dominated by pelagic taxa, but we could still identify littoral associated taxa, some of which were rare along the record.

**The role of littoral zones, the notion of diversity and its link to functionality, as well as the ratio of dominant versus rare species open possible leads to understand resilience mechanisms of deep lakes.**

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### 7.4.1 | THE ROLE OF LITTORAL ZONES

When present, submersed macrophytes in littoral zone provide crucial habitat for attached algae, invertebrates and fish. Furthermore, they impact the inter-specific interactions, by providing refuge against predators for instance (Burks *et al.*, 2001; Van de Meutter *et al.*, 2005). Nitrogen and phosphorus availability decreases in presence of littoral vegetation because macrophytes and attached algae participate in denitrification and oxygen production decrease phosphorus release from the sediment (Wetzel, 2001).

A spatial retrospective approach would maybe highlight the specific processes of littoral zone. In **Chapter 6**, we included lake perimeters as potential resilience factor. Our specific thinking was that high perimeter/surface ratio would indicate large presence of littoral zone. However, it is most likely that we would need a qualitative estimate of the state of the littoral zone, such as a percentage of natural versus disturbed littoral zone. In Lake Annecy (but also in Lakes Bourget and Geneva for instance), restoration works were carried out between 2011 and 2015 to restore reed beds (Figure 7.5). If the importance of the littoral zone in the resilience to climate variability is proved to be true, then the lake should follow its current trajectory and remain one of the resistant lakes in the peri-alpine area.

**Littoral cladoceran species are more diverse than pelagic ones** (Bjerring *et al.*, 2009)**. The complexity of the littoral food web may ensure resilience, due to traits redundancy** (Sanders *et al.*, 2018). **The idea that functional redundancy provides 'buffering' or**

**resilience against perturbations or environmental variability has been long established** (Walker *et al.*, 1999). **Dominant and minor species may be similar in their contribution to function, but will be different in response to events (see definition in Chapter 1), providing a 'reservoir of resilience' that allows maintenance of function under shifting conditions** (Walker *et al.*, 1999)**. Herein, we formulated the hypothesis that resilience to climate variability may have been lost with eutrophication. Palaeo-approaches offer the possibility to investigate these questions. I present below two other research leads: reconstruction of trait variance from palaeo-datasets and measure of resilience loss through shift between dominant and minor species.**

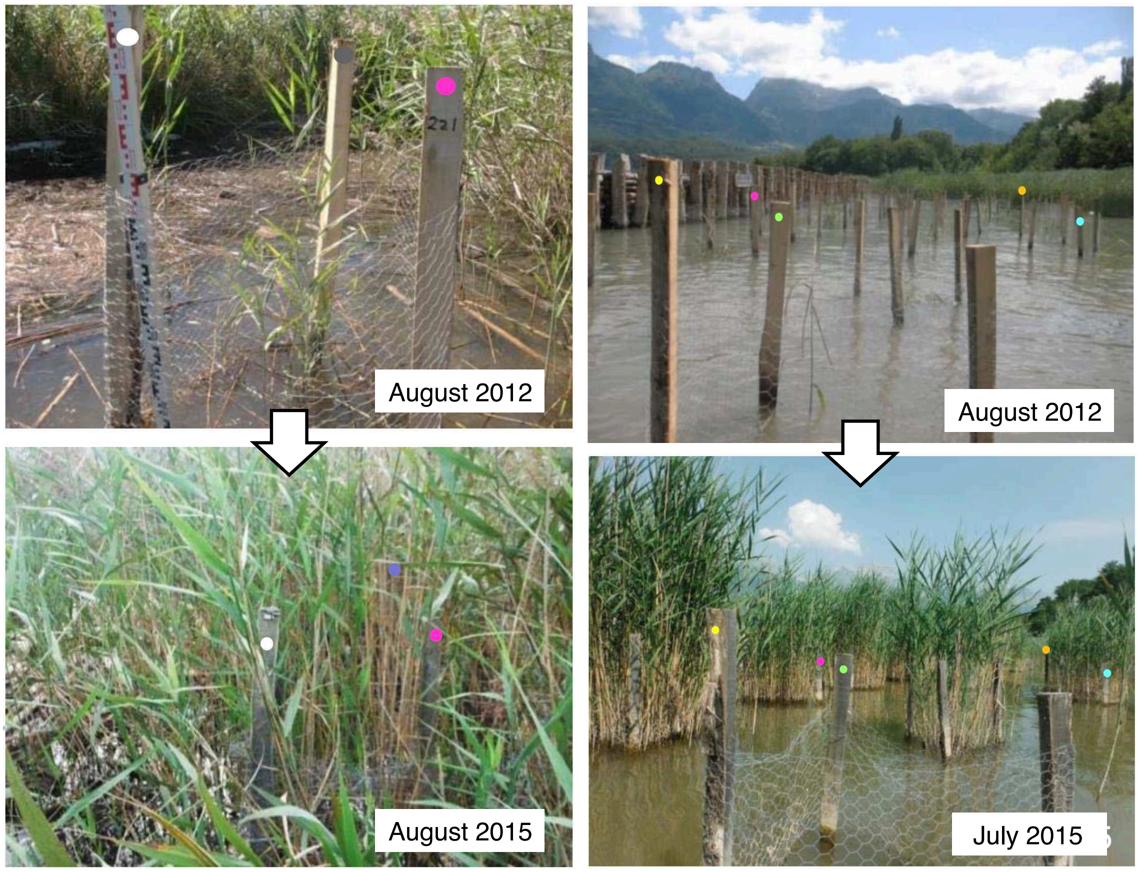

**Figure 7.5 I** Professed desire of Lake Annecy managers to restore its littoral zone.

Restoration works (planting, driftwood removing, protection against swell) were carried on between 2011 and 2015. The photos show reed bed evolution between summers 2012 and 2015 at two locations. Colour dots indicate same stakes in before/after pictures. Photo credits: SILA http://www.onema.fr/sites/default/files/pdf/11_Billet-ZanellaSILA_roselieresAnnecy.pdf

## 7.4.2 | FUNCTIONAL TRAIT APPROACH

In most environments, 3-4 abundant species can be enough to evaluate the quality of a system. Rare species hardly impact the results of quality status in bioindication because the indices were developed to minimise their contribution (Bigler, Gälman & Renberg, 2010). In good quality ecosystems, simplification of monitoring protocols could save time (Bigler *et al.*, 2010). However, rare species have another function in ecology, which is to replicate traits.

In the past years, trait approach has gained large interest among ecologists (e.g. Lavorel *et al.*, 2011; Gianuca, Pantel & Meester, 2016), and led to concrete management recommendations (e.g. Angeler *et al.*, 2014). Field observations conclude that there is an ecological redundancy of traits, and that this redundancy confer resilience to ecosystems (Walker *et al.*, 1999; Maestre *et al.*, 2012; Sanders *et al.*, 2018). Biodiversity maintain multifunctionality for both producer and consumer trophic levels in ecosystems that vary greatly in both abiotic and biotic properties (Cadotte, 2013; Fanin *et al.*, 2017). A negative consequence of biodiversity loss is reduced rates of ecosystem functions.

It is worth noting that traits include several layers e.g. *Daphnia* spp. and *Bosmina* sp. are pelagic grazers, but differ in size. They share the trait 'grazer' but they forage on different resources (Gianuca *et al.*, 2016).

In **Chapter 5**, we show that Lake Geneva cladoceran assemblage went from being composed by ~30% of the large *Sida crystallina* and ~65% of the small *Eubosmina longispina* to being almost exclusively composed of the large *Daphnia* spp.. Gianuca *et al.* (2016) experimentally showed that bi-stable grazer assemblage had a more efficient top-down control on algae development. It is possible that the pre-eutrophication community operated a more efficient top-down control on algae than the recent assemblage. Furthermore, the apparition of *Leptodora kindtii* now exerts a hold on pelagic grazers, which may impact their size and foraging capacity.

**Trait approach would constitute a relevant way to assess ecosystem health** (Gianuca *et al.*, 2016)**. This statement must be tempered by the fact the relationship between multifunctionality and biodiversity depends on the identity and number of measured functions** (Meyer *et al.*, 2017)**.**

### 7.4.3 | SHIFT BETWEEN DOMINANT AND MINOR SPECIES

In their recent paper, Doncaster *et al.* (2016) suggested that shifts between dominant ('keystone') and minor ('canaries' and 'weedy') species could be identified from palaeo-datasets and provide evidence for loss of resilience. The theory is explained in **Chapter 1**. They applied their method to the ecological trajectory of three lakes in China which diatoms and chironomids assemblage were reconstructed from sediment cores.

They hypothesise that interactions among species competing for similar resources sustain three functional categories: 'keystone' species that compensate slow self-replication by strong competitive ability; 'weedy' species that have opposite strategies (fast-replication but low competitive abilities); and 'canary' species that have both slow replication, and low competitive abilities. Doncaster *et al.* (2016) suggest that keystones prevail and canaries disappear when environmental conditions starts declining in quality. Above a certain threshold, faster replicating weedy species benefit from the competitive release and dominate the assemblage. In other word, vulnerability to extinction takes the order: slow-fugitive > slow-dominant > fast-subdominant.

They use nestedness metric (degree disorder, see **Chapter 1**) and Hill's diversity index, a measure for diversity that disproportionately favours common species (adapted for palaeo-datasets) to quantify the changes in abundance of the three groups. Consequently, the method does not require pre-assignment of specific groups.

We reproduced their methods and tested it on the cladoceran assemblages of Lakes Annecy, Bourget, Geneva, Lugano, and Varese. We discuss the preliminary interpretation for the latter, which trajectory is described in detail in **Chapter 4**.

Nestedness in Lake Varese decreases from 1900, reflected by an increase in degree disorder (Figure 7.6). It stabilizes following the major shift in both pelagic and littoral assemblage. Hill's diversity index increases along with disorder, and also stabilises from the 1950s. This pattern is similar to the one found by Doncaster *et al.* (2016) in the diatom assemblage of Lake Taibai (China) before the 1986 catastrophic shift.

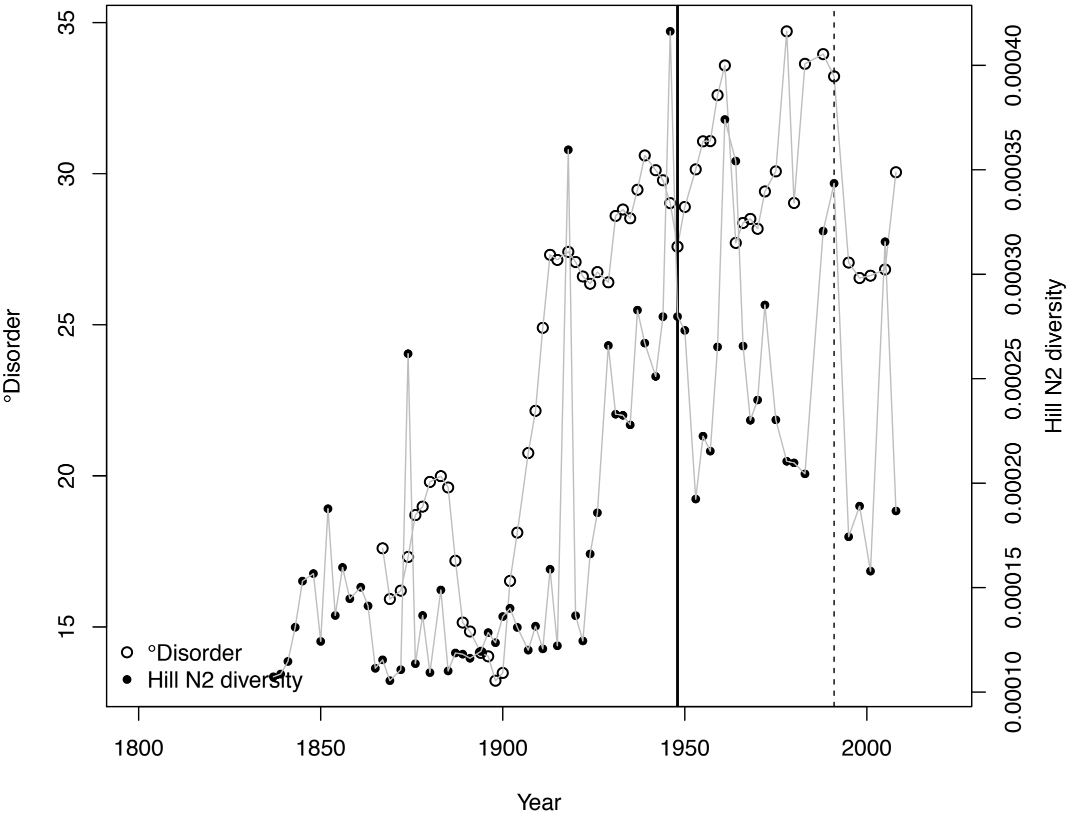

**Figure 7.6 I** Compositional disorder in Lake Varese cladoceran assemblage.

Nestedness of Lake Varese cladoceran community (open dots) calculated with a 15 sample window following Doncaster *et al.* (2016), along with Hill's diversity index (closed dots). Vertical plain and dashed lines respectively represent the main transition on PC1 and PC2, calculated with the change point method. The two main transitions reflect the transition in the 1940s as a response to eutrophication and the 1980s transition driven by climate warming (Chapter 4).

Correlations of degree disorder with biodiversity indicate community-level changes consistent with eutrophication from the 1920s to 1940s and hypereutrophication from the 1950s. The dynamic of indicators is more correlated during this pre-transition period than before the 1920s. It suggests a rising predominance of fast-replicating species following a demise of keystone species. The fact that degree disorder remains high after the transition, despite TP abatement, rather corroborates the new stable state hypothesis. Indeed, nested community before the 1920s was largely driven by littoral taxa. The high Hill's diversity index following the 1950s suggests an accumulation of frequently present (keystone) species against rare species.

The method cannot be applied across all systems we studied, as it requires a good time resolution, and a constant sampling. The main limitation concerns potential analytical error, if rare littoral taxa were missed during counting. We counted 400 remains when possible, which is adequate for such approach (see for diatoms: Bigler *et al.*, 2010). However, it would be more cautious to sample a littoral core to investigate these questions. Furthermore, Cladocera do not compete on the same resource (as diatoms do), so other dynamics could take place. It could also be interesting to investigate these dynamics on *Daphnia* spp. hybrid complexes as they display various strategy (e.g. *Daphnia galeata* invest more in sexual reproduction than hybrid, Keller *et al.*, 2007). Finally, the method developed by Doncaster *et al.* (2016) does not account for the number of species observed when calculating disorder metrics (Ulrich, Almeida-Neto & Gotelli, 2009).

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# Conclusion

## CONCLUSION

Physical, chemical, and biological processes are shaping ecosystems across great ranges of space and time scales (Levin, 1992). Feedback mechanisms confer stability (resilience) to ecosystems for a certain range of driver, until endpoints or tipping points are reached (Folke *et al.*, 2004; Wolkovich *et al.*, 2014). The generalised human impacts are pushing many ecosystems toward their limits (Vitousek *et al.*, 1997), so that regime shift (abrupt transitions and hysteretic response to the change in driver) have been reported in various ecosystems (Rocha, Peterson & Biggs, 2015). Climate change is bringing a large range of uncertainties into ecosystem trajectories, so that managers are urged to build ecosystems resilience (Epple & Dunning, 2014).

One of the most immediate challenges in conservation and applied ecology is to understand and predict the effects of multiple stressors (Schäfer & Piggott, 2018). Most observational datasets are limited to a small range of space and time scale, hampering our capacity to understand and forecast ecosystem trajectories (Wolkovich *et al.*, 2014; Schindler & Hilborn, 2015). In that respect, palaeolimnology grants the opportunity to reconstruct long-term ecological trajectories, providing a good baseline of expected changes under natural (non-modified by human) ranges of drivers variability (Spears *et al.*, 2017) .

Herein, we investigated the factor of ecological vulnerability, defined as the opposite of resilience, of deep peri-alpine lakes to climate change. Vulnerability can be described by the degree of changes in an ecosystem state that can be attributed to a given disturbance (Hodgson, McDonald & Hosken, 2015). We used a palaeo-ecological approach with a focus on diatoms and Cladocera, and quantified the amount of changes driven by local and global drivers.

We found that eutrophication has been the most important driver of peri-alpine lakes ecological trajectory at the scale of the past 1,250 years. Eutrophication triggered shifts in lakes, and restoration did not guarantee the littoral zone recovery. We could find the signature of climate change in every lake, which appeared to be modulated by the cumulative local perturbations.

Our approach shows that lakes vulnerability to key drivers (climate and eutrophication) can change over time. More precisely, local human impact (eutrophication) can increase lakes vulnerability to global impacts (climate change). The long-term insight shows that nature of forcing events (fast or slow, discrete or persistent) does not necessarily map clearly onto ecological responses, and confirm that the future is not a simple extrapolation of the past (Milly *et al.*, 2008; Wolkovich *et al.*, 2014; Schindler & Hilborn, 2015). In that respect, forecast must be taken carefully, and methods need to be developed to account for potential change in drivers.

Retrospective approach offers a good context to test ecological theories linked to slow non-stationary drivers such as climate change. Unsolved questions arose from this research, specifically on the impact of the littoral zone in conferring resilience to climate warming. The higher diversity provides a better context to detect early warnings of compositional changes (Doncaster *et al.*, 2016). Furthermore, we reached the limits of the modeling tools from the additive model family. While these models are accurate at relatively small time-scales (1-50 years), retrospective and forecast studies should systematically account for potential changes in vulnerability, based on the several lines of evidences that many processes are non-stationary (Milly *et al.*, 2008; Wolkovich *et al.*, 2014). Models for lake surface water temperature that integrate a potential for hysteresis (e.g. Toffolon *et al.*, 2014) could constitute a starting point for further researchs.

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# Appendix

## APPENDIX 1: COLLABORATIONS

This section presents the abstracts of four manuscripts I contributed on during the past 3.5 years (one submitted, three under preparation).

| **Title** | **Authors** |
|---|---|
| Storm impacts on lakes: (lower) frequency, rather than size, matters | Perga, Bruel, *et al.* (Under review) |
| *serac*: a R package for ShortlivEd RAdionuclide Chronology of recent sediment cores | Bruel & Sabatier (In prep.) |
| Human impact on planktonic and benthic communities at multiple trophic levels: The sedimentary record of Lake Joux, Switzerland | Monchamp, Bruel, *et al.* (In prep.) |
| Restoration of whitefish population in Lake Bourget: an historical analysis | Goulon, *et al.* (In prep.) |

# Storm impacts on lakes: (lower) frequency, rather than size, matters

Marie-Elodie PERGA (1,2), Rosalie BRUEL (2), Laura RODRIGUEZ (2), Yann GUÉNAND (2, 3), Damien BOUFFARD (4)

*Under review in Global Change Biology*

(1) University of Lausanne, Institute of Earth surface dynamics, 1015 Lausanne, Switzerland

(2) UMR CARRTEL, INRA, University Savoie Mont Blanc, Thonon les Bains, France

(3) SEGULA technologies, Le Bourget du Lac, France

(4) Department of Surface Waters Research and Management, Eawag-Swiss Federal Institute of Aquatic Science and Technology, Seestrasse 79, CH-6047 Kastanienbaum, Switzerland

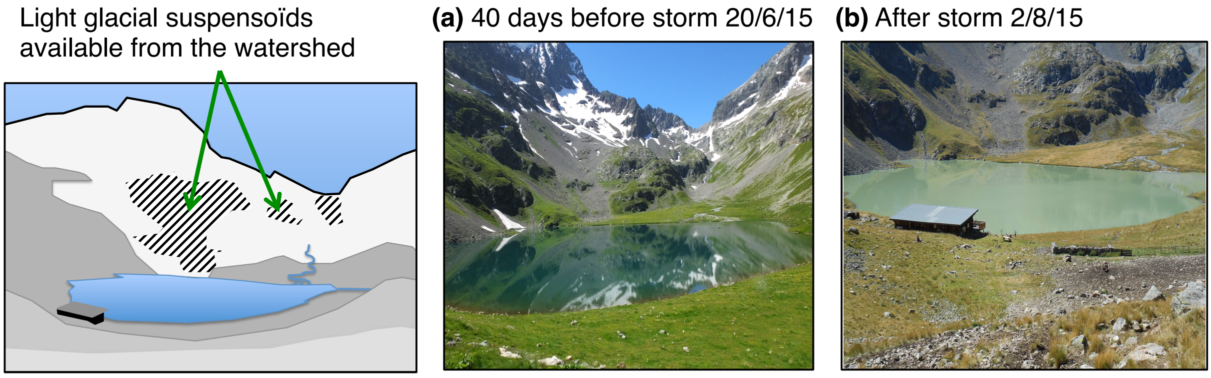
## Abstract

Intense episodic weather events could matter as much as gradual trends in mechanistically driving the long-term trajectories of ecosystems. High-altitude lakes are not only subject to exacerbated atmospheric warming but also highly exposed to intense episodic weather events. The future of these ecosystems under climate change might not be appropriately forecasted by only climate change trends, i.e., warming, if episodic events have the potential to deflect the seasonal trajectory of crucial physical and metabolic lake characteristics.

Combining high-frequency monitoring data over three open-water seasons with the modelling of the high-altitude Lake Muzelle (France), we show that rainstorms or windstorms, notwithstanding their intensity, do not trigger long-lasting consequences to the lake characteristics as long as they do not significantly modify the penetration of light in the lake. In contrast, turbid storms deeply and strongly modify the hydrodynamics and metabolism of the lake, considerably departing the lake from its seasonal trajectory. The long-lasting effects of the turbid storms could be mechanistically related to the inputs and persistence of very- light glacial suspensoids from the watershed. The occurrence of these turbid storms is not related to the intensities of windstorms or rainstorms. Instead, these events are promoted by both droughts during the weeks preceding the storm and less-frequent storm events, i.e., regional meteorological conditions forecasted for the upcoming decades. Thereby, even less frequent

storm events are projected to result in a stronger deflection of the lake ecological trajectories under climate change.

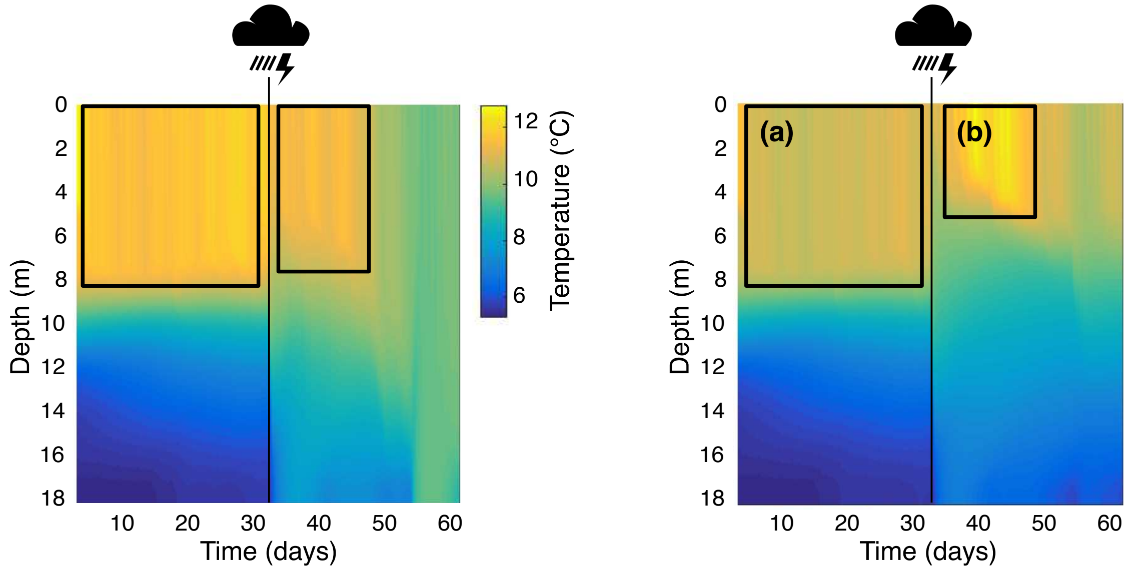
<u>*Specific contribution*</u>: *I worked on the quality control of the data. I ran the first analyses to detect storms based on their meteorological characteristics, and carried out a preliminary analysis of their impacts on the physics and deep oxygenation of the lake.*



**In the few days following a summer storm, two scenarios…**

**1.** Rapid sedimentation of particles
➔ Back to previous stratification pattern

**2.** Slow sedimentation of light particles
➔ New stable stratification pattern



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# ***serac*: a R function for ShortlivEd RAdionuclide Chronology of recent sediment cores**

Rosalie BRUEL(1), Pierre SABATIER(2)

*In preparation*

(1) CARRTEL, INRA, Université de Savoie-Mont Blanc, 74200 Thonon-les-Bains, France
(2) EDYTEM, Université de Savoie-Mont Blanc, CNRS, 73370, Le Bourget du Lac, France

## **Abstract**

Short-lived radionuclides are measured in surface sediment to provide geochronology over the past century. Age-depth models can be produced from $^{137}$Cs and $^{241}$Am activities using the peaks from the Chernobyl accident and the maximum nuclear weapon test, as well as from $^{210}$Pb$_{ex}$ activities derived sedimentation rates. The user needs to ensure that any instantaneous event was removed from the sequence, before finally computing the age-depth model. These different steps require a certain expertise and understanding of lake sedimentation.

We developed a code, *serac*, that allows the user to compute age-depth model and provide an output graph, as well as age model in a text file, on the free open-source statistical software R. *serac* ensure the reproducibility of age-depth model, and grant the possibility to test several $^{210}$Pbex model (CFCS, CIC, CRS) and sedimentation hypothesis (change in sedimentation rates, instantaneous deposits, slumps, etc.). By tacking several case studies including lakes in different environments, we provide different situations a user may be confronted to.

The rising number of sediment cores and the need to correlate among them requires reproducible methods. *serac* is an user friendly function that accompanies the scientist in age model computation for the last century.

Specific contribution: *I wrote the code and used it to generate the new age models presented in the thesis. I will now implement the other models (right now the model is only designed for constant flux: constant sedimentation hypothesis) and write the corresponding materials sections in the manuscript.*

# Human impact on planktonic and benthic communities at multiple trophic levels: The sedimentary record of Lake Joux, Switzerland.

Marie-Eve MONCHAMP (1-2), Rosalie BRUEL (3), Victor FROSSARD (3), Suzanne MCGOWAN (4), Marlène LAVRIEUX (5), Moritz MUSCHICK (6), Marie-Elodie PERGA (3, 7), Nathalie DUBOIS (2, 8)

*In preparation*

(1) Department of Aquatic Ecology, Eawag, Swiss Federal Institute of Aquatic Science and Technology, Switzerland;

(2) Department of Surface waters – Research and Management, Eawag, Swiss Federal Institute of Aquatic Science and Technology, Switzerland;

(3) INRA, Université de Savoie Mont-Blanc, UMR CARRTEL, Thonon-les-bains, France

(4) Faculty of Social Sciences, School of Geography, University of Nottingham, United Kingdom

(5) Department of Environmental Science, University of Basel, Switzerland

(6) Department of Fish Ecology & Evolution, Eawag, Swiss Federal Institute of Aquatic Science and Technology, Switzerland

(7) Faculté des géosciences et de l'environnement, Institut des dynamiques de la surface terrestre, Université de Lausanne, Switzerland

(8) Geological Institute, Department of Earth Sciences, Swiss Federal Institute of Technology Zurich (ETHZ), Switzerland

## Abstract

Most palaeoreconstruction studies focus on one taxonomic group and often are limited to fossil organisms leaving biological remains in the sedimentary archive of lakes. By combining traditional palaeolimnological proxies (e.g. cladoceran, chironomid and fish remains, phytoplankton pigments) with DNA-based methods applied to sedimentary ancient DNA and historical records of human presence, it is possible to investigate the long-term changes in

multiple groups of lacustrine organisms to evaluate the impact of humans across the entire food-web. Here, we reconstructed the trajectories of planktonic and benthic organisms in a lake with a well-known history of human settlement and land-use over ca.1000 years. The results show a striking and unprecedented ecological change, which has occurred in the middle of the twentieth century at all taxonomic levels investigated (bacteria, zoo- and phytoplankton, chironomids, cladocerans and fish, following several centuries of relatively stable community composition and diversity. Simultaneous palaeoreconstructions of the past dynamics at multiple levels of the lake's food-web have the potential to uncover shifts in biodiversity and ecosystems function and to inform us about the factors governing these ecological changes in a conservation and management perspective.

<u>Specific contribution:</u> *I prepared and counted the samples for Cladocera subfossil remains and ran the first analyses for this group. I help building the age-depth model through MSCL correlation between the working cores and the reference core.*

## Restoration of whitefish population in Lake Bourget: an historical analysis

Chloé GOULON [(1)], Emilien LASNE [(1)], Orlane ANNEVILLE [(1)], Rosalie BRUEL [(1)], Isabelle DOMAIZON [(1)], Sébastien CACHERA [(2)], Alexis CHAMPIGNEULLE [(1)], Jean GUILLARD [(1)]

*In preparation*

(1) UMR CARRTEL, INRA, University Savoie Mont Blanc, Thonon les Bains, France

(2) CISALB, 73000 Chambéry, France

### Abstract

Lake Bourget whitefish (*Coregonus lavaretus*), an indigenous fish that is at the southern limit of its range, has been dramatically impacted by eutrophication. In the 1950s catches were close to 90 tons and decreased to less than 1 ton by the 1970s. Important remediation work has been carried out to reduce phosphorus inputs to the lake and a major supportive breeding program was undertaken. Today, Lake Bourget is returning to oligotrophic conditions and whitefish catches are equivalent to the pre-eutrophication period. However, in recent decades, annual mean air temperatures significantly increased possibly impacting the fish population. The objective of this study is to analyse the long-term whitefish population dynamics and to identify the main environmental factors involved in their evolution.

Palaeolimnolgy data combined with recent observations have been correlated to the whitefish catches over a 70-year time series. Contribution of the main forcing factors (climate change, reoligotrophication and stocking) was explored using a Generalized Additive Model. According to our results, phosphorus has been the main parameter influencing whitefish dynamics, with the stocking effort also contributing to the restoration of the population. However, recently, rising temperatures have likely impacted whitefish dynamics, raising concern for the future of the population.

<u>*Specific contribution:*</u> *I worked on GAM analyses and interpretations with CG.*

# APPENDIX 2: LISTS OF FIGURES, TABLES AND BOXES

## LIST OF FIGURES

## LIST OF TABLES

## LIST OF BOXES

# APPENDIX 3: C.V. (JUNE 2018)

# Rosalie Bruel (Ph.D., French, 26 years old)

✉ 9 rue Henri Reynaud, 13290 Les Milles, France
📧 rosaliebruel@gmail.com
☎ +33 621 815 728
Ⓢ rosalie.bruel

Last update: June 3, 2018

## Education

**2014-2018** **University Savoie-Mont Blanc, Chambéry, France**
Ph.D. student, Ecology.

**2012-2014** **University of Pau et Pays de l'Adour, Anglet, France**
M.A., Aquatic Ecology and Hydrobiology.

**2011-2012** **Napier University, Edinburgh, Scotland (UK)**
B.A. of Science with Distinction, Environmental Biology.

**2009-2011** **University Aix-Marseille, Digne-les-bains, France**
BTEC Higher National Diploma, Environmental Biology.

## Research

**04.2018** **CARRTEL (University Savoie Mont-Blanc), Thonon-les-bains, France**
Study collaborator. Supervisor: V. Frossard.
Project: SIGNALE.
I sub-sampled a 70 cm core from Lake Tignes (FR) for ancient DNA and biological remains. I analysed the samples for Cladocera sub-fossils.

**10.2014-09.2017** **CARRTEL (INRA/University Savoie Mont-Blanc), Thonon-les-bains, France + CNR-ISE, Verbania-Pallanza, Italy (7 months international stay)**
Ph.D. candidate. Supervisor: M.-E. Perga.
Project: "Eutrophication legacy on peri-alpine lakes ecological vulnerability to climate change".
I reconstruct the long-term (80 to 1500 years) succession of zooplankton communities in heavily anthropised peri-alpine lakes. My objective is to distangle the impacts of climate change and local human forcings, testing for theoritical non-linear properties of systems and loss of resilience.
Collaboration with researchers from various backgrounds (Ecology, Paleolimnology, Sedimentology): EDYTEM, ISTerre (FR), University of Geneva, University of Lausanne, EAWAG, ETH Zurich (CH), CNR-ISE (IT)

**2014** **Edytem & Asters, Le Bourget-du-lac, France**
Master thesis. Supervisors: F. Arnaud, E. Malet (Edytem), C. Birck (Asters).
Project: "Constraints and contributions of high-frequency sensors in the monitoring of ecosystems: the example of Lake Anterne watershed"
During the first part of the project, I cleaned (QA/QC) and compiled the data from Lake Anterne monitoring program (weather, in-lake sensors, river station, soil sensors). Then, I used the data to give the first picture on the seasonal dynamics of this high-altitude lake (e.g. mixing periods). Finally, I coded on R a routine to detect summer extreme events (extreme wind, rain, or combination of both) from high-frequency data, and investigated the impact on the physico-chemistry of the lake.

**2013** **Halieutic Ressources Laboratory, Ifremer, Anglet, France**
Master thesis. Supervisor: N. Caill-Milly.
Project: "Impact of environmental factors on manila clam (*Venerupis philippinarum*) morphology in Arcachon Bay (France)"
I looked at the relationships between manila clam morphology and environmental conditions (extracted from MARS-3D model) to find the potential best protected area in Arcachon Bay.

# Courses

**2015 International Summer School in limnology, Bolshie Koty (RU)**
“Lake Ecosystems under Pressure, Processes and Impacts”.
**2014 International Summer School in limnology, Evian-les-Bains (FR)**
“Lake Ecology and Temporal Dynamics”.
**2014 NETLAKE Workshop, Action COST ES1201, Uppsala (SE)**
“Automated Monitoring and High-Frequency Data Analysis”.

# Awards and Fellowships

**PAGES**
Grant to attend 2<sup>nd</sup> EcoRe3 workshop in Salt Lake City, US (2018) ($850)
Grant to attend 5<sup>th</sup> PAGES Open Science Meeting in Zaragoza, Spain (2017) (200€)
**Explo’RA Doc, Grant awarded by Region Auvergne Rhone-Alpes**
Funding for international stay at the Institute for Ecosystem Studies (CNR-ISE, Verbania-Pallanza, IT), 2016 (6 months) (4260€) .
**Doctoral School SISEO**
Funding to support the participation to an International Summer School (in Russia), 2015 (800€) .
**Ph.D. Grant awarded by the University Savoie Mont-Blanc**
Awarded for 3 years (2014-2017) (60500 €)
**International student grant awarded by the Student Award Agency for Scotland**
Grant awarded to cover Napier University tuitions fees (2011-2012) (£1820)
**Student Awards**
- Best Poster, Ph.D. students Day, Doctoral School SISEO, 13 November 2015
- Best Presentation, International Summer School in Limnology, August 2014

# Scientific Life

**2017-05-22 March for Sciences, Thonon-les-bains (FR)** - Organisation team co-leader of Thonon-les-bains Satellite March. Contact with authorities for autorisation request. Public relation via local newspapers, Twitter, Facebook. Organisation and animation of meetings.
**2016-09-30 European Researchers Night, Verbania-Pallanza (IT)** - Introduction to paleolimnology with the paleo-team of the CNR-ISE.
**2015-10-11 "Fête des sciences", Thonon-les-bains (FR)** - Member of the organization committee. Creation of a children play-book.
**2015-07 9th Symposium for European Freshwater Sciences, Geneva (CH)** - Student volunteer.
**2015-06 NETLAKE Workshop, Evian-les-bains (FR)** - Support in the organization.

# Skills

**Languages**: English (advanced), French (native)
**Main interest / theoretic knowledge**: Limnology, Freshwater ecology, Transitions in ecosystems (drivers, dynamics, linearity vs. non-linearity), climate change, multi-lake analysis
**Paleolimnology**: Core sampling and sub-sampling (regular+DNA protocol), Sediment dating (radioelements, paleomagnetism), Age models (clam), XRF analysis
**High-frequency**: QA/QC (GLEON programs: Data Standardizer, B3), buoy deployment
**Evaluation of community diversity**: Sampling strategy, Taxonomy (cladoceran sub-fossils, river macro-invertebrates), Pigments analysis (HPLC)
**Statistics**: R, uni- and multivariate analysis of ecological data, linear and non-linear models, temporal series
**Scientific Communication**: R, Python (Graphics), QGIS, LaTeX, Microsoft Office Suite, Zotero

# Publications

## Publications in peer reviewed international scientific journals

**2018** **Bruel, R.**, Marchetto, A., Bernard, A., Lami, A., Frossard, V., Sabatier, P., Perga, M.-E. (In press — Freshwater Biology) Seeking alternative stable states in a deep lake. DOI: 10.1111/fwb.13093

**Subm.** **Bruel, R.**, Girardclos, S., Marchetto, A., Kremer, K., Lami., A., Crouzet, C., Reyss, J.-L., Sabatier, P., Perga, M.-E. (Under review — Global Change Biology) Lakes in the Anthropocene are more vulnerable to climate variability.

Perga, M.-E., **Bruel, R.**, Rodriguez, L., Guénand, Y., Bouffard, D. (Under review — Global Change Biology) Storm impact on lakes: size matter more than frequency.

**In prep.** **Bruel, R.**, Marchetto, A., Milan, M., Tolotti, M., Lami, A., Nevalainen, L., Manca, M., Dubois, N., Sabatier, P., Perga, M.-E. (In prep.) Quantitative approach to lakes ecological vulnerability to climate change.

**Bruel, R.**, Sabatier, P. (In prep.) *serac*: a R function for Short-livEd RAdionuclides Chronology of recent sediment cores.

Monchamp, M.E., **Bruel, R.**, Frossard, V, McGowan, S, Lavrieux, M, Muschick, M, Perga, M.-E., Dubois, N. (In prep.) Human impact on planktonic and benthic communities at multiple trophic levels: The sedimentary record of Lake Joux, Switzerland.

Goulon, C., Lasne, E., Anneville, O., **Bruel, R.**, Domaizon, I., Cachera S., Champigneulle A., Guillard, J. (In prep.) Restoration of whitefish population in Lake Bourget: an historical analysis.

## Theses

**2018** **Bruel, R.** Eutrophication legacy on peri-alpine lakes ecological vulnerability to climate change. CARRTEL, INRA/University Savoie-Mont Blanc. PhD program, University Grenoble Alpes.

**2014** **Bruel, R.** Constraints and contributions of high-frequency sensors in the monitoring of ecosystems: the example of Lake Anterne watershed. Asters/Edytem. Master DynEA, UPPA. 25p + Supplementary Materials.(French version available upon request)

**2013** **Bruel, R.** Impact of environmental factors on manila clam (*Venerupis philippinarum*) morphology in Arcachon Bay (France). Ifemer. Master DynEA, UPPA. 50p + Supplementary Materials (French version available upon request)

## Reports

**2014** **Bruel, R.**, Malet E. Lake Anterne's monitoring (north-eastern French Alps). Documentation about the data and metadata. Edytem. 22p. (English version available upon request)

**Bruel, R.** Tinytag Explorer – Dispositifs de mesures Tinytag installés dans le cadre du suivi des lacs dans les Alpes françaises. Guide de l'utilisateur. 16p. (French version available upon request)

**Bruel, R.** Data Standardizer – Standardisation des données capteur. Guide de l'utilisateur. 11p. (French version available upon request)

**Bruel, R.** B3 – Compilation de données haute-fréquence et outil de contrôle des données. Guide de l'utilisateur. 24p. (French version available upon request)

## Communications

### International Seminar, Conference, Workshop

**2018** **Bruel, R.**, Alric, A., Marchetto, A., Girardclos, S., Marchetto, A., Kremer, K., Frossard, V., Perga, M.-E. Size structure of zooplankton grazer community to infer lake ecological resistance towards climate variability. *EcoRe3 2nd Workshop.* Salt Lake City, UT (US), 8-10 May 2018 **(Presentation)**

**2017** **Bruel, R.**, Marchetto, A., Bernard, A., Lami, A., Frossard, V., Sabatier, P., Perga, M.-E. Littoral habitats display evidence for alternative stable states even in a deep lake. *SEFS 10.* Olomouc (CZ), 2-7 July 2017 **(Presentation)**

**Bruel, R.**, Marchetto, A., Bernard, A., Lami, A., Frossard, V., Sabatier, P., Perga, M.-E. Operational assessment of regime shifts: application to the long-term ecological trajectory of a hollow lake under multiple forcings. *OSM Pages 2017.* Zaragoza (ES), 9-13 May 2017 **(Presentation)**

**Bruel, R.**, Girardclos, S., Marchetto, A., Kremer, K., Crouzet, C., Reyss, JL., Sabatier, P., Perga, ME. Another Side of the Anthropocene: humans increased ecosystem vulnerability to climate variability. *OSM Pages 2017.* Zaragoza (ES), 9-13 May 2017 **(Poster)**

**2016** **Bruel, R.** Lakes vulnerability to climate change modulated by human local forcings: ongoing studies and future collaboration with ISE. Seminari Limnologici del Istituto per lo Studio deli Ecosystem (CNR), Verbania Pallanza (IT), 13 May 2016 **(Seminar)**

**Bruel, R.**, Bernard, A., Marchetto, A., Lami, A., Frossard, V., Sabatier, P., Perga, M.-E. Nutrient, not climate change, drives a new equilibrium in the cladoceran assemblage of a deeper lake (Italy). *XIV Subfossil Cladocera Workshop.* Levico Terme (IT), 5-8 April 2016 **(Presentation)**

**2015** **Bruel, R.**, Birck, C., Sentinel lakes: a network for the study and management of mountain lakes in the French Alps. *SEFS 9.* Geneva (CH), 5-10 July 2015 **(Presentation)**

**Bruel, R.**, Girardclos, S., Kremer, K., Perga, ME. Comparison of current and medieval planktonic responses to atmospheric warming in Lake Geneva. *SEFS 9.* Genève (CH), 5-10 July 2015 **(Poster)**

**2014** **Bruel, R.**, Arnaud, F., Malet, E., Birck, C., Perga, M.E. NETworking Lake observatories in Europe. Lake Anterne, Netlake site in France. *Netlake workshop.* Erken (SE), June 2014 **(Poster)**

### National (FR) Conference

**2015** Bouffard, D., **Bruel, R.**, *et al.* Modelling as a tool to understand high-altitude lakes: Lake Anterne case study. Bourg d'Oisans, 9-10 November 2015 **(Presentation by DB)**

**Bruel, R.**, Kremer, K., Girardclos, S., Perga, M.-E.. Comparison of Lake Geneva zooplankton responses to current and medieval atmospheric warming. *15e Congrès Français de Sédimentologie.* Chambéry, 13-15 October 2015 **(Presentation)**

**2014** **Bruel, R.**, Arnaud, F., Malet, E., Birck, C. Treatment of high-frequency monitoring data: contributions on understanding lakes dynamics – The example of Lake Anterne. *5e rencontres scientifiques et techniques, Réseau Lacs Sentinelles.* Aix-en-Provence, 27-28 November 2014 **(Presentation)**

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### References

**Marie-Elodie Perga**
Associate Professor
University of Lausanne (UNIL)
Lausanne, Switzerland
marie-elodie.perga@unil.ch, +41-21-692-4323

**Aldo Marchetto**
Permanent Researcher
Istituto per lo Studio degli Ecosistemi
Verbania-Pallanza, Italy
a.marchetto@ise.cnr.it, +39-0323-518331

**Pierre Sabatier**
Lecturer
Edytem, CNRS, University Savoie Mont-Blanc
Chambéry, France
pierre.sabatier@univ-smb.fr, +334-7975-8867