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Unravelling nutrient dynamics in Sierra Nevada lakes through sediment-water interactions

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ABSTRACT

Unravelling nutrient dynamics in Sierra Nevada lakes through sediment-water interactions

Global change stressors are anticipated to trigger eutrophication and deteriorate water quality in high mountain lakes. To accurately predict the future of these vulnerable aquatic systems, research must adopt a holistic approach that integrates sediment-water interactions–processes often underestimated in oligotrophic high mountain lakes compared to external drivers. This paper provides a historical review of the primary chemical, physical, and biological mechanisms governing sedimentary phosphorus (P) mobilization and highlights how these dynamic interactions are influenced by global change. Subsequent sections focus on two Sierra Nevada lakes (Río Seco and La Caldera, Granada, Spain) with contrasting watershed and hydrological characteristics to assess how desiccation and re-flooding influence sedimentary P dynamics, and water quality. Furthermore, the study explores sedimentation and resuspension processes, emphasizing their crucial role in coupling planktonic and benthic communities. Lake desiccation decreases sedimentary P adsorption capacity due to the reduction in fine mineral fractions (rich in iron and aluminium oxides) and organic matter. Long-term data from La Caldera over 20 years confirm significant P increases in lake water during droughts. Overall, understanding how water level fluctuations (WLFs) influence the biogeochemistry in these high-mountain lakes, and Mediterranean wetlands more broadly, is pivotal for accurately forecasting the responses of inland waters within the evolving global change scenario.

KEY WORDS: sediment, nutrient, desiccation, reflooding, Sierra Nevada lakes, global change.

RESUMEN

Interacción agua-sedimento como factor determinante de la dinámica de los nutrientes en lagos de Sierra Nevada (España)

Los factores de estrés asociados al cambio global se prevé que intensifiquen la eutrofización y deterioren la calidad del agua en los lagos de alta montaña. Para predecir con precisión la evolución de estos ecosistemas vulnerables, es esencial adoptar un enfoque holístico que incorpore las interacciones sedimento-agua, tradicionalmente subestimadas en lagos oligotróficos frente a los factores externos. Este estudio revisa los principales mecanismos químicos, físicos y biológicos que controlan la movilización del fósforo (P) sedimentario y analiza cómo dichos procesos dinámicos se ven modulados por el cambio global. Se presentan resultados de dos lagos de Sierra Nevada (Río Seco y La Caldera, Gra-

nada, España), con cuencas y regímenes hidrológicos contrastantes, para evaluar los efectos de la desecación y la posterior reinundación sobre la dinámica del P sedimentario y la calidad del agua. Los resultados muestran que la desecación reduce la capacidad de adsorción del P debido a la pérdida de fracciones minerales finas (ricas en óxidos de Fe y Al) y materia orgánica. Datos de largo plazo (20 años) en La Caldera confirman incrementos significativos de P disuelto durante períodos de sequía. En conjunto, estos hallazgos subrayan la importancia de las fluctuaciones del nivel del agua (WLFs) en la regulación de la biogeoquímica de los lagos de alta montaña y, por extensión, de los humedales mediterráneos, aportando claves fundamentales para anticipar la respuesta de las aguas continentales ante escenarios de cambio global.

PALABRAS CLAVE: *sedimento, nutrientes, desecación, reinundación, lagos de Sierra Nevada, cambio global.*

INTRODUCTION

High mountain regions, by virtue of their altitudinal gradients and relative isolation from direct human activities, serve as critical sentinels of global climate change (Beniston, 2003). This inherent sensitivity makes them invaluable natural laboratories for monitoring and understanding the far-reaching consequences of a changing climate (Tito et al., 2020). Within these mountain regions, aquatic ecosystems, particularly high-altitude lakes, represent ecosystems characterized by their pristine waters and great biological uniqueness, rendering them highly sensitive to environmental deterioration of both regional and global stressors (Adrian et al., 2009, Catalan et al., 2006, Guerrero, 2021).

These ecosystems are particularly vulnerable to global change associated with the Anthropocene - a proposed geological epoch characterized by significant human impact on Earth's systems (Crutzen, 2002) - so they are intrinsically linked to several planetary boundaries (Richardson et al., 2023, Rockstrom et al., 2009, Steffen et al., 2011, 2015a, b), particularly those related to climate change, biogeochemical cycles and biosphere integrity. This unprecedented environmental change can destabilize the delicate balance of these lakes, causing alterations in their physical and chemical conditions, and in their biological communities (e.g. Adrian et al., 2009, Cabrerizo et al., 2017, Carrillo et al., 2017). The interplay of modified precipitation patterns, altered hydrological regimes, and increased atmospheric deposition of nitrogen, phosphorus (P), and other pollutants fundamentally reshapes the dynamics and compromises the ecological functioning of lakes (Adrian et al., 2009, Havens & Jeppesen, 2018, Hessen et al., 2024, Woolway et al., 2020). As Tammeorg et al. (2024) highlight, numerous predictive models have been developed to project the interactive effects of these stressors on ecological quality (e.g., Richardson et al., 2018, Spears et al., 2021). For instance, projected scenarios indicate a potential 1.5- to 1.9-fold increase in the economic costs of algal blooms in the UK by the 2050s (Jones et al., 2020), emphasizing the tangible consequences of these combined pressures. Currently, the ecological integrity of European freshwater bodies faces a severe challenge, as highlighted by the latest environmental reports which highlights a critical need for focused conservation efforts, particularly for pristine high-mountain ecosystems that provide essential ecosystem services (EEA, 2025). The situation becomes even more concerning given the geographic location and geological history of the Sierra Nevada (southern Spain). These high-mountain lakes are exposed to several environmental stressors simultaneously: climatic anomalies linked to a climate-change hotspot in the Mediterranean region, high UV radiation, increased Saharan atmospheric dust deposition, and allochthonous nutrient inputs (Zamora et al., 2022). Complex and diverse methodological approaches, encompassing paleolimnological investigations, observational studies, and field and laboratory experimental manipulations, have unequivocally demonstrated the profound impact of global change drivers on these specific lakes (e.g., Medina-Sánchez et al., 2022, Pérez-Martínez et al., 2022, Reche et al., 2022). Paleolimnological records have revealed significant changes in the lakes and their catchments starting subtly over a century ago and accelerating in the 1960s and 1970s, concurrent with rising regional air temperatures, declining precipitation, and increased

Saharan dust deposition (Pérez-Martínez et al., 2022). As a result, pronounced changes in the composition of aquatic communities and a recent increase in algal biomass have been registered. This nature of change has been interpreted as a result of a lengthening of the ice-free period and a rise in lake water temperature, alongside reduced water availability in their catchments and an intensification of summer droughts. Observational and experimental approaches have further revealed an interannual decline in the percentage of mixotrophic algae coupled with a proportional increase in strict autotrophs (Carrillo et al., 2017). Furthermore, a weakening of bacterivory has been observed in favor of autotrophic processes, reinforcing commensalism between algae and bacteria via the release of dissolved organic carbon (González-Olalla et al., 2018). These structural and functional changes are closely linked to an increase in mean summer air temperature and the rising intensity and frequency of Saharan aerosol-dust depositions (Carrillo et al., 2017, González-Olalla et al., 2018).

The environmental trajectories observed in the Sierra Nevada reflect a global phenomenon observed across the world's major mountain ranges, highlighting the need for a cross-regional perspective. In the Alps, for instance, Sommaruga (2015) found that the melting of glaciers and ice sheets fundamentally alters the light climate and nutrient stoichiometry of high-altitude lakes, triggering profound shifts in planktonic community structures as water transparency and mineral turbidity fluctuate. Similar climate-driven pressures are evident in the Andes, where the combination of warming and land-use changes increases sedimentation and nutrient loading (Anderson et al., 2011), mirroring the anthropogenic pressures identified in Mediterranean summits. Furthermore, evidence from the Carpathians, specifically the Tatra Mountains, suggests that even remote lakes are transitioning toward higher productivity due to rising temperatures and increased ice-free durations despite declines in certain industrial pollutants (Kopáček et al., 2011). These global parallels reinforce the status of high-mountain lakes as consistent indicators of the Anthropocene and emphasize that the findings in the Sierra Nevada are part of a broader, global response of alpine aquatic ecosystems to environmental forcing.

At this point it is clear that the geographical location of Sierra Nevada's high-mountain lakes, coupled with altered precipitation regimes and increased temperatures driven by climate change, is inducing substantial changes in their stored water volume. In this sense, it has been recognized that although Mediterranean water bodies are naturally characterized by extreme water level fluctuations (WLFs) due to irregular precipitation patterns (Álvarez-Cobelas et al., 2005), global climate change is projected to intensify this variability by shortening precipitation seasons and increasing summer drought incidence (Coops et al., 2003), as Pérez-Martínez et al. (2022) have already noted for Sierra Nevada lakes. These amplified WLFs are particularly pronounced in closed-basin lakes, where water levels are directly governed by the precipitation-evaporation balance (Marsh & Lesack, 1996). Despite the growing recognition of the ecological relevance of WLFs in lentic ecosystems, their influence on ecosystem responses remains poorly understood, with contrasting findings reported (Turner et al., 2005, White et al., 2008).

WLFs have serious consequences for the biogeochemistry of aquatic ecosystems (de Vicente, 2021). Current research focuses on two key aspects. On the one hand, WLFs influence an ecosystem's capacity to act as a source or sink of greenhouse gases (e.g., Alfadhel et al., 2024). More specifically, Fennesy et al. (2017) identified that the ability of wetlands to store carbon depends on interconnected factors operating at various scales and hydrologic disturbances, such as drainage and shorter periods of inundation, which increase soil desiccation and the oxidation of organic carbon, consequently releasing carbon dioxide into the atmosphere (Bridgham et al., 2006). A clear example of the strong link between greenhouse gas fluxes and hydrological conditions comes from Alfadhel et al. (2024), who showed that a Mediterranean saline lake acts as a significant carbon sink under wet conditions, but CO_2 uptake drops by over 80% during prolonged droughts. Hydrological shifts, however, also influence other greenhouse gas fluxes, such as nitrous oxide (N_2O) from denitrification processes, and potentially other nitrogen oxides (NO_X). On the other hand, the eventual impact of alternating drying and re-flooding cycles on nutrient dynamics is particularly interesting, as it can ultimately determine water quality by promoting P release or retention by the sediment. The overall effect of alternating dry and wet periods on P availability is lake-specific, thus requiring site-specific research. Despite the foreseeable importance in nutrient-limited oligotrophic lakes, such processes remain poorly studied in these ecosystems (de Vicente et al., 2010a).

Apart from WLFs which will surely strengthen the benthic-pelagic coupling, there are several reasons why sediment-water interactions, responsible for internal nutrient supply, may play a special role in these unique ecosystems. Firstly, as they represent remote and pristine systems where the external load of nutrients is extremely low (Cruz-Pizarro & Carrillo, 1996, Morales-Baquero et al., 1999, Villar-Argaiz et al., 2001), any change in sediment and water interactions is likely to impact nutrient dynamics. Secondly, sedimentary P mass is much higher than P mass contained in lake water and thus, any shift in the physical-chemical conditions that release sedimentary P strongly affect water quality. As an illustration, de Vicente et al. (2010a) showed that a TP concentration of 0.5 mmol/m^3 in Río Seco (Pulido-Villena et al., 2003) corresponds to the water-extractable PO_4^{3-} in the uppermost 1 cm of sediment per square meter of lake bed. They also determined that this layer held 17.6 mmol/m^2 of iron-bound PO_4^{3-}, a sedimentary mobile P fraction. Similarly, the equivalent numbers for La Caldera are 0.245 and 8.42 mmol/m^2 for water extractable and iron-bound PO_4^{3-}, respectively, compared to 0.08 mmol/m^3 in the water column (Pulido-Villena et al., 2003). A third argument that confirms the relevance of lake sediment in the dynamics of nutrients is the high surface to maximum depth ratio in these lakes, especially in Río Seco, that undoubtedly favours resuspension events of the lake sediment.

Global change stressors are expected to trigger eutrophication and deteriorate water quality in Sierra Nevada lakes, highlighting a major blind spot in many environmental assessments which is the tendency to focus almost exclusively on external drivers while overlooking the crucial internal ecosystem processes. To truly grasp and accurately predict the future state of these vulnerable aquatic ecosystems requires a holistic approach that recognizes the pivotal role of sediments. In this context, this paper first provides a historical overview of the primary chemical, physical and biological mechanisms governing the mobilization of sedimentary P forms and its dynamics sediment-water interactions in response to global change. Subsequent sections transition to a more detailed examination of the high-mountain lakes of Sierra Nevada. Two lakes within the National Park in Granada, Spain (La Caldera and Río Seco) were selected for study due to their differences in both watershed and hydrological features (e.g., Morales-Baquero et al., 1999, 2006, Reche et al., 2001). The paper then explores the changes occurring within the sediments of these lakes upon exposure to desiccation and re-flooding conditions, and their subsequent impact on sedimentary P dynamics by using simplified laboratory experimental approaches. Next, observational evidence is presented to illustrate how WLFs directly affect the water quality of the Sierra Nevada lakes. Finally, the paper examines sedimentation and resuspension processes, highlighting their role in maintaining a strong coupling between the planktonic and benthic communities.

BACKGROUND TO THE CHALLENGES OF SEDIMENT AND WATER INTERACTION

While initial research by Einsele (1938) and Mortimer (1941, cited in Mortimer, 1971) simplified P exchange across the sediment-water interface to exclusively chemical oxidation-reduction processes, current understanding recognizes the diverse and intricate factors and mechanisms governing benthic nutrient dynamics (Boström et al., 1982, de Vicente, 2004, Golterman, 2001). In sediments, P exists in many forms including covalently bound in organic matter (OM), sorbed as inorganic phosphate ion (PO_4^{3-}) onto inorganic metal oxides (particularly poorly crystalline iron and aluminium oxides), and coprecipitated with carbonates (Boström et al., 1988, Reddy & DeLaune, 2008). Thus, the flux of P between sediments and overlying waters is potentially controlled by multiple processes, including the balance between biotic uptake and microbial mineralization, sorption and desorption, and mineral coprecipitation and dissolution. Importantly, each of these different forms of sedimentary P is mobilized from the sediment through distinct chemical, physical or biological processes, each influenced by different environmental conditions (Fig. 1). The traditional emphasis on chemical processes over biological ones (e.g., OM mineralization) in P cycling studies might stem from the use of P fractionation methods that poorly isolate sedimentary organic P (org-P). In the 80s, this problem was tackled by Golterman & Booman (1988) and De Groot & Golterman (1993) who developed a separation method of P bound to iron hydroxides (P~FeOOH) and P bound to calcium carbonate (P~$CaCO_3$) by using specific (chelating) extractants instead of operative extractants such as NaOH and HC1. As a first result they demonstrated that the organic pool is much larger than previously assumed, as NaOH and HC1 hydrolyse a large part of the org-P (which is then measured as inorganic P). Similarly, de Vicente et al. (2003) compared two of the most prevalent sequential extraction methods, representing contrasting approaches: operational (defined by the extraction steps, not specific compounds, as in Pardo et al., 1999) and functional (Golterman, 1996). Results from two shallow eutrophic lakes evidenced that while the total amount of sedimentary P extracted by the two methods was quite similar, significant differences in the proportion of inorganic versus organic P was achieved depending on the method. Again, the extraction with aggressive compounds (HCl and NaOH) used in Pardo et al. (1999) method causes an underestimation of the organic P fraction due to its partial conversion into inorganic forms. Beyond methodological limitations, Golterman (2001) argued that a misunderstanding of the seminal work by Einsele (1938) and Mortimer (1941) has led to an inaccurate conceptualization of P release under anoxic conditions. He challenged the traditional FeOOH chemical reduction mechanism, contending that the association between FeOOH and P actually stabilizes the complex, making it thermodynamically more resistant to reduce than FeOOH alone (Golter-

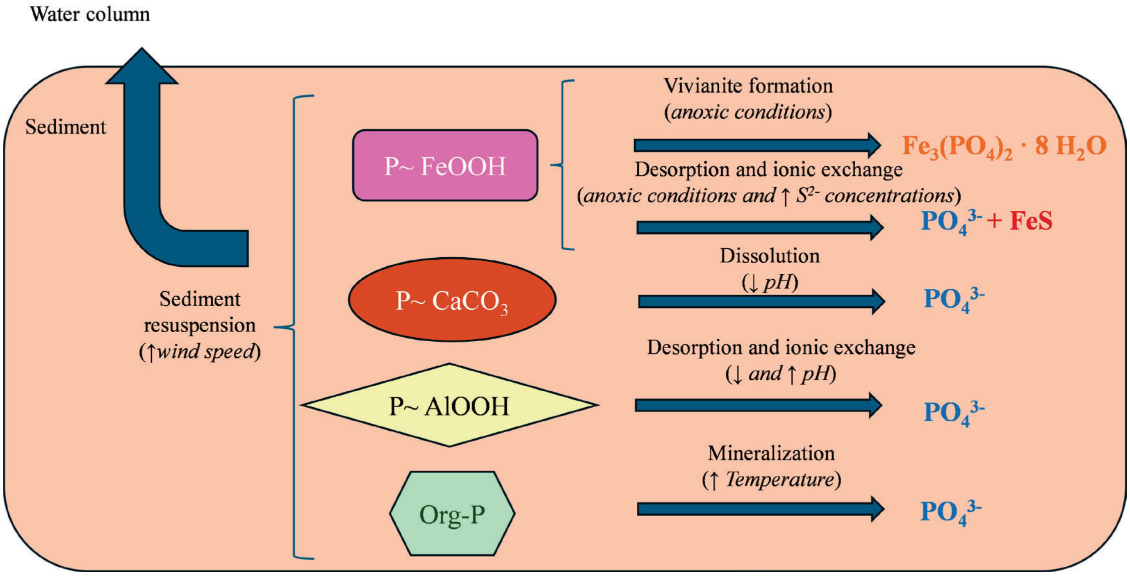


Figure 1. Processes involved in the release of phosphate ions into the interstitial sediment water from different P_{sed} fractions (modified from Boström & Pettersson, 1982). The formation of vivianite is also included, although it does not lead to the release of phosphate ions. The conditions that favour each mechanism are indicated in italics. Please note that phosphate bound to iron, calcium carbonate and aluminium are denoted as P ~ FeOOH, P ~ $CaCO_3$ and P ~ AlOOH, respectively. *Procesos implicados en la liberación de ion fosfato al agua intersticial del sedimento desde las diferentes fracciones de P_{sed} (modificado de Boström & Pettersson, 1982). También se incluye la formación de vivianita, aunque no produce la liberación de iones fosfato. Las condiciones que favorecen cada mecanismo se indican en cursiva. Por favor, nótese que el fosfato unido al hierro, carbonato cálcico y aluminio se representa como P ~ FeOOH, P ~ $CaCO_3$ y P ~ AlOOH, respectivamente.*

man, 1984, 2001). Furthermore, Golterman noted the unexpected coexistence of FeS and FeOOH in natural sediments and suggested that the reducing power in the hypolimnion is typically insufficient to reduce more than a small fraction of the total FeOOH. In agreement, Prairie et al. (2001) found that only in a few lakes did the stoichiometry of released products align with expectations from the Fe-reduction hypothesis. Beyond these arguments against an anoxic P release driven by FeOOH reduction and FeS formation, De Groot (1991) and Golterman (2001) also proposed that vivianite [$Fe_3(PO_4)_2 \cdot 8\ H_2O$] formation could actually limit this release in oxygen-deprived environments. Under anoxic conditions, the balance between vivianite and FeS formation, and thus between P retention and release, is contingent upon various factors such as PO_4^{3-} and sulphide levels. Although vivianite is redox-stable and may act as a substantial P sink in anoxic sediments (e.g., Rothe et al., 2015), van Kuppevelt et al. (2025) showed through mesocosm experiments with sediment cores from Lake Arendsee (Germany) that elevated sulphate reduction rates enhance P mobilization from vivianite-rich layers, increasing soluble reactive P in the water column. This research underscores the importance of sulphur cycling in internal P loading and suggests that increased sulphate inputs could exacerbate eutrophication by releasing P from buried vivianite. Although a low formation of vivianite is typically limited in oligotrophic, oxic lakes, its occurrence has been reported in such environments (e.g., Rothe et al., 2016, Slomp et al., 2013, Vuillemin et al., 2020).

Even though Fe mineral sorption is often the dominant form of P retention in soils and sediments, other chemical processes can also control sediment–water P exchange (e.g., Boström et al., 1988). In calcareous sediments, PO_4^{3-} can co-precipitate with or sorb to calcium carbonate ($CaCO_3$) minerals, retaining large amounts of P (Hamilton et al., 2009). These calcareous minerals tend to precipitate under alkaline, warm conditions and dissolve under acidic conditions (Boström et al., 1988). Golterman, with his strong foundation in chemistry, was undeniably one of the most significant limnologists to research the stability of apatite-bound P. Golterman (2001), building on earlier work by Stumm & Morgan (1970), showed that anoxia-induce CO_2 production lowers pH, promoting apatite dissolution and partial P release, some of which re-adsorb onto FeOOH. As Golterman (2001) recognized that this acidity-related release did not occur in Mortimer's studies, as the Lake District waters are very soft, and in Mortimer's days the P-loading was still low and apatite absent. Finally, there is a last form of inorganic P present in lake sediments which is associated with aluminium oxides (P~AlOOH). Although it is naturally found in low concentrations, it can be mobilized through desorption and ion exchange mechanisms governed by pH (e.g., Hem & Roberson, 1967). From a practical point of view, the stability of P~AlOOH has gained significant attention due to the application of aluminium in combating eutrophication (e.g., Cooke et al., 2005, de Vicente et al., 2008a, Reitzel et al., 2005, Rydin & Welch, 1998, Welch & Cooke, 1999). Actually, the first aluminium treatment dates back to the 1970s in the Swedish lake Långsjön (Jernelöv, 1971), and the technique has since been applied in over 200 lakes worldwide.

Apart from chemical mechanisms, P exchange across the sediment-water boundary is drastically influenced by physical and biological processes. Aerobic P release is particularly significant in shallow, wind-exposed systems, where wind-induced resuspension transports both PO_4^{3-} and particulate P that can later desorb (Peters & Cattaneo, 1984, Søndergaard, 1993), sometimes in quantities sufficient to affect water quality (Ryding & Forsberg, 1977). Furthermore, microbial activity is also recognized as a crucial influence on the mobility of P within sediments (Böstrom et al., 1988, Clavero et al., 1999). This inherent complexity highlights the necessity for ad hoc research considering not only the chemical composition and the physicochemical conditions of the water column but also the fractional composition of sedimentary P (López, 1991).

Sediment-water interactions are dynamic and significantly impacted by global change (de Vicente, 2021). Figure 2 summarizes major drivers: (i) air temperature; (ii) solar radiation, (iii) precipitation, (iv) wind speed, and (v) human activities. Elevated temperatures accelerate microbial activity, potentially leading to faster rates of OM decomposition in the sediment and altered nu-

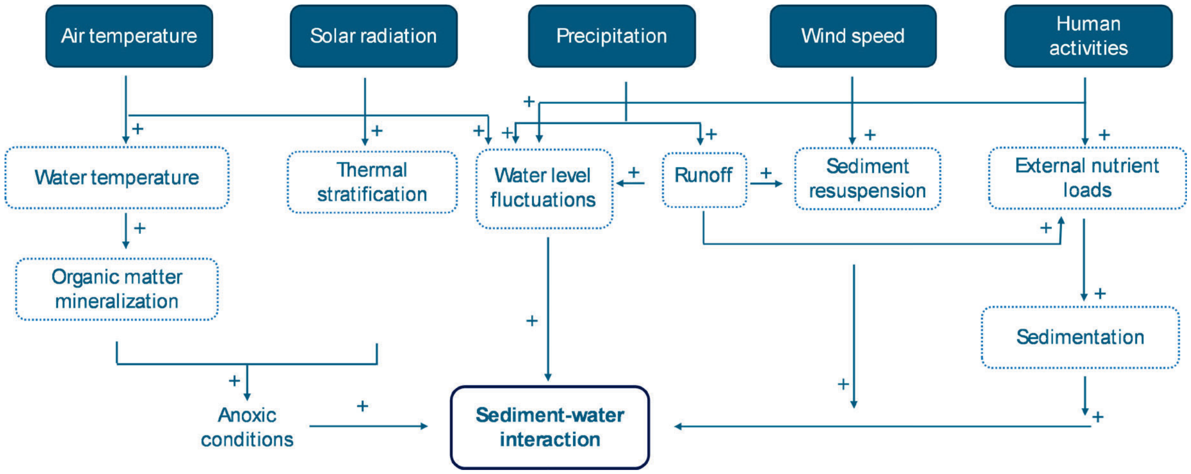


Figure 2. Key global change drivers affecting sediment-water interactions (modified from de Vicente, 2021). *Principales factores de cambio global que afectan la interacción sedimento-agua (modificado según de Vicente, 2021).*

trient cycling pathways (e.g., Golterman, 1990). Cimate-driven increases in solar radiation reduce mixing, leading to earlier and longer summer stratification in the future (Mesman et al., 2021, Woolway & Merchant, 2019, Woolway et al., 2021). Therefore, the impacts of temporary stratification, though less studied, could explain unexpected ecological events (e.g., Søndergaard et al., 2023), such as algal blooms in Lake Balaton (Istvánovics et al., 2022) or loss of larval mayfly recruitment during short hypoxic periods in Lake Erie, affecting yellow perch fisheries (Bridgeman et al., 2006). Climate change is expected to increase the occurrence and severity of both droughts and extreme flow events, causing dramatic WLFs (Barnett et al., 2005, Milly et al., 2005). Altered wind regimes (e.g., Azorín-Molina et al., 2016, Collins et al., 2013, IPCC, 2021) will also directly impact sediment resuspension. Finally, global warming facilitates the spread of cultivated land into high-altitude areas, and together with poor land-use planning and urbanization, elevate external nutrient inputs and subsequent sedimentation rates (Yao et al., 2017). Long-term mesocosm studies confirm that increased nutrient input enhanced sediment accumulation and sedimentary P concentrations, except for P bound to aluminium and humic matter (Saar et al., 2022). Moreover, over-exploitation of water resources further amplifies annual and interannual WLFs exceeding natural ranges, particularly in hydroelectric reservoirs (e.g., Hirsch et al., 2014). Collectively, these global change-driven stressors will dramatically impair the water quality of aquatic ecosystems by enhancing sediment-water interaction, though the ultimate impact hinges on the system's inherent characteristics such as morphology, size, and geographical location.

FLUCTUATING DRY AND WET PERIODS AS DRIVERS OF SEDIMENTARY PHOSPHORUS DYNAMICS

While initial studies evaluating the impact of desiccation on sedimentary P release date back to the 1970s (Bartlett & James, 1980, Brookes et al., 1982, Dommergues & Mangenot, 1970), such research has gained renewed significance in the aforementioned context of global change. Among the first comprehensive studies in Mediterranean wetlands, De Groot & Fabre (1993) and De Groot & Van Wijck (1993) combined laboratory and field approaches in a Camargue freshwater march (France), revealing notable changes in the P-fractions and sedimentary P-adsorption capacity. In the 1980s, Fabre (1988) examined reservoirs with water level fluctuations up to 22 m, using factorial experiment to evaluate key factors including sediment origin, sediment moisture, refilling rates, and water origin. More recently, Baldwin

(1996) who tested the effects of exposure to air and subsequent drying on the P adsorptive characteristics of sediments in a small eutrophic reservoir in New South Wales (Australia).

In this century, Batzer & Sharitz (2006) highlighted the significant influence of wetting and drying cycles on wetland biogeochemical processes, emphasizing the tight links between hydrology, biogeochemistry, and microbial ecology. They identified some crucial factors such as the duration of dry phases between inundation events, the rate of water level increase during flooding, and water retention times in wetland. Kinsman-Costello (2012) further reviewed the effects of sediment desiccation and re-flooding on P dynamics in wetlands, a topic of growing relevance as environmental managers manipulate wetland hydrologic regimes to counteract the adverse consequences of past hydrologic and other human impacts. This includes re-flooding historically drained areas for wetland restoration (Zedler, 2003), constructing new wetlands for water quality enhancement (Kadlec & Wallace, 2009), and applying temporary draining and re-flooding for purposes such improved water quality, weed control (Kinsman-Costello, 2012) and crop management (e.g., rice, blueberries).

A literature review reveals contradictory findings, spanning from increased P adsorption after drying (Barrow & Shaw, 1980, De Groot & Fabre, 1993, Haynes & Swift, 1985) to eutrophication following sediment reflooding (Baldwin, 1996), highlighting the complexity of chemical, physical, and biological transformations at play (de Vicente et al., 2010a). In this sense, figure 3 summarizes the main sediment changes during drying that can increase or reduce sediment's capacity to adsorb P. For instance, Barrow & Shaw (1980) proposed that drying can decrease the hydration of FeOOH gels in soils, increasing particle surface area of FeOOH and PO_4^{3-} adsorption, whereas other studies have shown that particle-size shifts towards larger particles in dried sediments reduce PO_4^{3-} affinity (Qiu & McComb, 2002, Selig, 2003, Twinch, 1987).

Desiccation also induces various chemical alterations in sediments and soils, particularly in FeOOH pools driven by increased oxygen availability. The capacity of sediments to adsorb PO_4^{3-} is strongly predicted by the amount of poorly crystalline Fe and/or Al oxides and oxyhydroxides, which have higher sorption capacity than crystalline forms (Darke & Walbridge, 2000, Williams et al., 1971). Generally, flooding dry soils tends to increase these poorly crystalline Fe and Al oxides (Darke & Walbridge, 2000, Zhang et al., 2003), whereas drying previously flooded sediments reduces them (Baldwin, 1996, Qiu & McComb, 2002, Twinch, 1987). Consequently, drying can both enhance PO_4^{3-} sorption by oxidizing reduced Fe minerals, but reduce it by increasing crystallinity, with the net effect being time-dependent (Baldwin & Mitchell, 2000). This process likely begins with the rapid oxidation of Fe^{2+} salts (e.g, sulphides, carbonates, phosphates) in previously anoxic zones into amorphous FeOOH, which

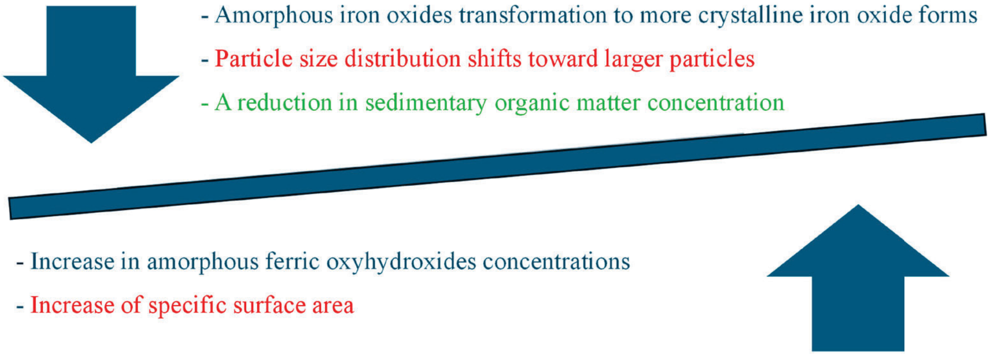


Figure 3. Main chemical (blue color), physical (red color) and biological (green color) changes responsible for the reduction or the increase in maximum P adsorption capacity in sediments under desiccation. *Principales cambios químicos (color azul), físicos (color rojo) y biológicos (color verde) que provocan un aumento o una reducción en la capacidad máxima de adsorción de P en sedimentos durante la desecación.*

possesses a high affinity for PO_4^{3-} (De Groot & Van Wijck, 1993). Prolonged air exposure ages these amorphous FeOOH phases into more crystalline mineral forms (Baldwin, 1996, Lijklema, 1980), although the reversibility upon re-wetting is debated. The initial sediment composition also dictates the duration required for these shifts, with ferrous sulphide-rich sediments needing longer drying. It is also important to note that while Al oxides and oxyhydroxides are redox-insensitive, drying and flooding cycles can still alter their crystallinity, likely because the accumulation of OM in flooded areas inhibits the crystallization of both Al and Fe minerals (Darke & Walbridge, 2000, Kodama & Schnitzer, 1977, 1980, Schwertmann, 1966).

Beyond abiotic transformations, biological processes significantly influence PO_4^{3-} dynamics in hydrologically dynamic wetlands (Batzer & Sharitz, 2006, Sparling et al., 1985). While research has traditionally focused on physico-chemical reactions, Gilbert et al. (2014) identified OM decomposition, rather than FeOOH reduction, as the primary driver of PO_4^{3-} exchange during desiccation. Accelerated OM mineralization under aerobic conditions (Reddy et al., 2000) reduces organic P in dried sediments, yet OM also enhances PO_4^{3-} retention through amorphous mineral stabilization (Darke & Walbridge, 2000), cation bridging with Ca and Mg (Brady & Weil, 2008, Bruland & Richardson, 2006, Novak & Watts, 2006), and by inhibiting the recrystallization of Fe and Al compounds, thereby maintaining high sorption capacity (Darke & Walbridge, 2000).

As Kinsman-Costello (2012) and de Vicente (2021) pointed out, our understanding of sediment-water P exchange following re-flooding largely stems from three approaches: (i) laboratory assessments of PO_4^{3-} sorption capacity in field-sampled or experimentally treated sediments and soils, (ii) laboratory re-flooding experiments, and (iii) ecosystem-scale monitoring of hydrologic changes, often in historically drained areas. However, comparisons across these approaches are often challenging due to substantial variations in study design and methodology. For instance, some research involves laboratory drying and re-flooding of sediments collected from already inundated field sites, while others examine sediments from dry or historically drained areas subjected to laboratory re-flooding. In our opinion, whenever possible, sampling from in situ desiccations is preferred for realism, capturing physical, chemical, and biological changes, while laboratory desiccation is useful for process-specific studies. Inconsistent reporting of desiccation and the limited range of sediment types further constrain the generalizability of findings for wetland management.

The first approach, following the methodology of Froelich (1988), involved laboratory adsorption experiments using wet and dry sediments. The resulting experimental data were subsequently fitted to isotherms (e.g., Freundlich or Langmuir) to derive key parameters, such as the maximum P adsorption capacity and the desorption term (e.g., de Vicente et al., 2010a). To identify the underlying controlling mechanisms, these parameters were statistically correlated with independent sediment properties, including texture, mineralogical composition, and OM content.

In Sierra Nevada lakes, de Vicente et al. (2010a) investigated the effects of the extreme 2005 drought, documenting a significant decline in PO_4^{3-} sorption capacity along littoral-to-dry land transects in both La Caldera and Río Seco. Spearman's rank correlation showed that maximum P adsorption capacity (Q_{max}, Langmuir isotherm) was positively correlated to OM, fine particles (< 20 μm), and oxalate-extractable (amorphous) Fe and Al oxides (Fe_{ox} and Al_{ox}) (Fig. 4). Specifically, desiccated sediments had lower PO_4^{3-} adsorption capacities, linked to reductions in these components, driven by: (i) wind exposure removing fine, metal-oxide-rich particles, and (ii) elevated temperatures and oxic conditions accelerating OM mineralization.

The impact of WLFs on P availability is frequently assessed through laboratory re-flooding of fresh versus dried sediments. In Sierra Nevada lakes, de Vicente et al. (2010a) observed that re-wetting air-dried sediments from La Caldera and Río Seco under oxic conditions released PO_4^{3-} to the overlying water, coinciding with a progressive decrease in Feox during the first three months, suggesting a time-dependent crystallization of FeOOH, a less documented phenomenon compared to the stable behavior observed for Al_{ox}.

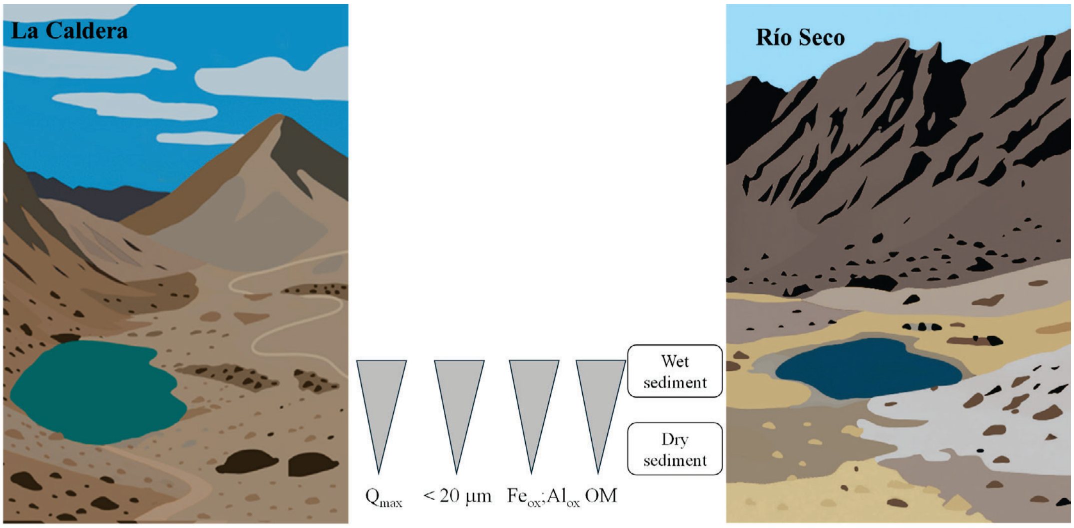


Figure 4. Impact of desiccation on surface sediment properties in La Caldera and Río Seco. *Impacto de la desecación sobre las propiedades del sedimento superficial de las lagunas de La Caldera y Río Seco.*

The latest methodological approach monitors alterations in water chemistry, specifically P availability, when dried sediments are re-flooded. Studies show that flooding historically drained sediments causes release of P to surface waters (e.g., Ardón et al. 2010, Kinsman-Costello et al., 2014, Wong et al. 2011), sometimes producing a pulse of inorganic nutrients known as the "birch effect" (Baldwin & Mitchell, 2000, Birch, 1960, Wilson & Baldwin, 2008). This approach has clear limitations in Sierra Nevada lakes, as neither La Caldera nor Río Seco have fully dried. The following section explores how WLFs specifically influence the ecosystem dynamics of these high-mountain lakes.

OBSERVATIONAL EVIDENCE OF THE EFFECTS OF WATER LEVEL FLUCTUATIONS ON NUTRIENT DYNAMICS OF LA CALDERA

The study of drought and refilling (D&R) cycles in the Sierra Nevada lakes became feasible in the early 1990s, coinciding with the widespread drought that affected Spain from 1991 to 1995 (Llamas, 1997). During this period, La Caldera recorded its lowest depth, reaching only 1.8 m in 1995, followed by a rapid recovery to 14 m in 1996, offering a unique opportunity to assess the effects of severe hydrological fluctuations on nutrient dynamics and planktonic communities (Medina-Sánchez et al., 1999, Villar-Argaiz et al., 2002 a, b). Subsequent droughts in 1999 and 2004-2006 (Estrela, 2006) further corroborated these observations (García-Jurado et al., 2011, 2012). García-Jurado et al. (2012) compiled these studies to analyze the effects of recurrent drought conditions and WLFs on the plankton community (bacterial, phytoplankton, heterotrophic nanoflagellates and zooplankton) and nutrient availability (DIN, TN, TP, DIN:TP) in La Caldera (Fig. 5). Based on precipitation values and the water levels, these authors distinguished three periods within a 20-year study (1986 - 2006): (i) >1200 mm and >10 m; (ii) 425-1200 mm and 4-10 m; and (iii) <425 mm and <4 m. Results are shown in figure 5, revealing that changes associated with these periods affected lake volume, expanding the littoral sediments exposed to desiccation and enhancing sediment-water interactions. Recurrent droughts and subsequent rehydration periods significantly impact macronutrient dynamics (N and P), dissolved organic carbon (DOC; Yu et al., 2020), and plankton communities, with important implications for lake stability and ecosystem homeostasis under climate change (García-Jurado et al., 2012). DIN, TN, and the DIN/TN mass ratio, did not exhibit any trend, whereas TP in-

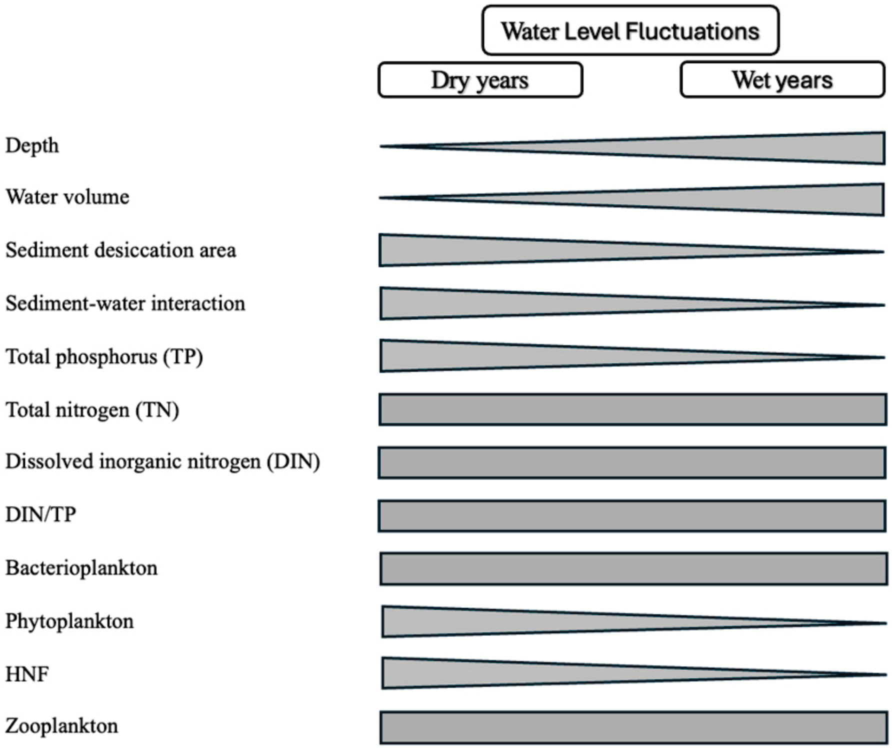


Figure 5. Significant trends in environmental and biotic variables associated with water level fluctuations (WLFs) in La Caldera from 1986 to 2006. Data from García-Jurado et al. (2012). *Tendencias significativas en las variables ambientales y bióticas asociadas a las fluctuaciones del nivel de agua (WLFs) en la laguna de La Caldera entre 1986 y 2006. Datos de García-Jurado et al. (2012).*

creased during droughts. Bacteria and zooplankton showed no significant differences between periods, while phytoplankton and heterotrophic nanoflagellates (HNF) increased under low-water conditions. An analysis of the differences from the long-term mean (DLTM; White et al. 2008) revealed a significant inverse relationship between water deph and total P ($DLTM_{TP}$), heterotrophic flagellates ($DLTM_{HNF}$), and zooplankton ($DLTM_{zoo}$), indicating that prolonged low-water periods corresponded to higher TP and plankton abundances, whereas TN, phytoplankton, and bacteria showed no such relationship.

Therefore, in Sierra Nevada lakes, TP increases significantly during drought; despite high variability, concentrations consistently exceed those recorded in wet years, likely due to sediment resuspension (de Vicente et al., 2010b) and/or the deposition of P-enriched atmospheric dust (Jiménez et al., 2018, Morales-Baquero et al., 2006, 2013). Conversely, no significant differences were observed across wet and dry periods for TN. However, these patterns may not apply to all lakes in Sierra Nevada, owing to the inherent properties of each lake (Morales-Baquero et al., 1999), highlighting the need for further research to fully understand drought impacts.

Increased P during droughts strongly affects the autotroph: heterotroph (A:H) ratio, which falls below one in dry years and exceeds one in wet years (García-Jurado et al., 2011, Medina-Sánchez et al., 1999). Bacteria showed no significant differences between dry and wet years, while HNF increased in dry years. Phytoplankton abundance rose during droughts, with no differences in the DLTM analysis. Conversely, zooplankton abundance remained stable during the inter-period comparison but showed clear differences towards a greater abundance during the dry periods in the DLTM analysis. To explain these disparities, Cabrerizo et al. (2017) highlighted that, in addition to D&R cycles, these patterns are also influenced by the pulses of atmospheric nutrient inputs. Intense nutrient inputs favour phytoplankton biomass over bacteria and mixotrophic flagellates. Similarly, strong dust deposition increases sediment nutrients, altering prokaryotic community composition and affecting biogeochemical and biodiversity (Castellano-Hinojosa et al., 2024). Under ongoing climatic and global change, projected increases in temperature and Saharan dust deposition in lakes of Sierra Nevada are expected to further impact the ecological condition.

SEDIMENTATION AND RESUSPENSION PATTERNS IN OLIGOTROPHIC LAKES

Challenging the traditional perception of inland waters as mere passive pipes conveying organic and inorganic carbon from land to sea, Cole et al. (2007) demonstrated that they actively participate in the global carbon cycle, storing land-derived carbon in sediments, emitting CO_2, and transporting carbon to the ocean. Sedimentation of carbon and nutrients is a key ecological process in aquatic ecosystems, transferring particulate matter from euphotic or coastal zones to deeper areas, and linking planktonic and benthic communities (de Vicente et al., 2005, 2022). This process holds substantial practical implications for both ecosystem monitoring and infrastructure management, as sedimentation rates, which correlated with trophic status (e.g., Tartari & Biasci, 1997), progressively diminishes water storage capacity. Current sedimentation rates, estimated at 1% annually, have already claimed 32.8% of global reservoir storage (Ren et al., 2021), and without new construction, half of the world's 6· 1012 m^3 capacity could be lost by 2050 (Sumi, 2018).

Gross sedimentation rates are typically estimated using cylindrical traps with an aspect ratio (H:D) > 6 to minimize resuspension (Bloesch, 1982, Bloesch & Burns, 1980). The rates are later calculated based on the collected mass, trap area, and exposure time (de Vicente et al., 2005, 2008b, 2009, 2010b). This approach provides key insights into OM mineralization, sediment resuspension, and mineral precipitation (Kalff, 2002). In La Caldera and Río Seco, daily settling rates during the 2005-2006 ice-free period ranged from 0.38 to 1.18 g DW m^{-2} d^{-1} ($p > 0.05$), consistent with values reported for other oligotrophic systems (Tartari & Biasci, 1997). This confirms the positive correlation between trophic status and sedimentation flux (de Vicente et al., 2005, Gálvez et al., 1991); being these values yet far lower than rates in eutrophic Mediterranean reservoirs (66.6 g DW m^{-2} d^{-1}; de Vicente et al., 2022).

In shallow lakes, upward resuspension of unconsolidated sediments is also a key process (Bloesch, 1995, Weyhenmeyer et al., 1995), driven by continuous wave action (de Vicente et al., 2010c, Kristensen et al., 1992, Weyhenmeyer & Bloesch, 2001), which mobilizes both particulate and dissolved P (e.g., Reddy et al., 1996, Søndergaard et al., 1992) and accelerates chemical equilibrium with the water column (Golterman, 2004). While resuspension rates are often estimated by comparing deep and shallow traps (Gardner, 1977, Kleeberg, 2002), this method can be unreliable in shallow lakes where resuspended material may reach the upper water column (Bloesch, 1994), though they have successfully identified resuspension factors in two shallow Spanish lakes (de Vicente et al., 2010c). In Sierra Nevada lakes (La Caldera and Río Seco), extreme shallowness precluded trap-based estimates; however, in other systems like Medina Lake (Spain), alternative methods using chemical tracers such as total iron (TFe) revealed resuspension exceeding 40% during no-inflow periods (de Vicente et al., 2012).
Lake sediment resuspension is modulated by both external forces (e.g., wind speed) and internal site characteristics, including morphometry (e.g., water depth, lake fetch), sediment composition (e.g., granulometry, OM content) and biological activity (e.g., bioturbation, macrophytes coverage). In a comparative study of two adjacent shallow lakes (Honda and Nueva), de Vicente et al. (2010c) revealed that morphometry and sediment characteristics significantly modulate wind-driven resuspension. Thus, Lake Honda's shallower basin and finer sediments resulted in higher resuspension rates compared to the deeper, sandier, and macrophyte-stabilized Lake Nueva (de Vicente et al., 2010c). Consequently, greater resuspension in Lake Honda promoted OM mineralization, yield-

ing similar C:P ratios between surface sediments and settling material, whereas Lake Nueva's distinct C:P ratios indicated minimal contribution from resuspended particles to the settling flux (de Vicente et al., 2003, 2010c).

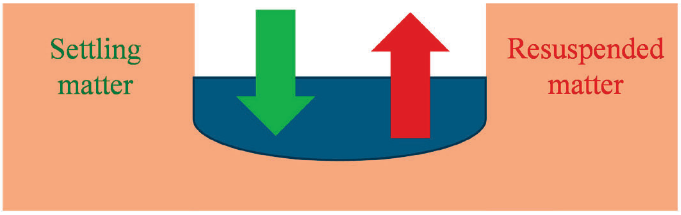
In La Caldera and Río Seco resuspension was not directly quantified due to the shallow depths, but differences were on morphometry: over 90% of Río Seco is shallower than 2 m, whereas most of La Caldera exceeds 2 m (de Vicente et al., 2010b), and Río Seco's hollow coefficient (maximum depth divided by the square root of the lake area) is over three times lower, indicating more frequent sediment resuspension.

Sedimentation and resuspension strongly modulate nutrient availability in the water column, with settling OM replenishing nutrients via mineralization during summer stratification (Gálvez & Niell, 1993) or acting as a P sink in P-limited lakes (de Vicente et al., 2005). In Sierra Nevada, this impact is lake-specific: resuspension increased PO_4^{3-} concentrations in Río Seco but not in La Caldera, suggesting that frequent resuspension events in Río Seco may alter P availability (de Vicente et al., 2010b). Finally, the chemical composition of settling and resuspended matter followed similar trends in La Caldera and Río Seco, as shown in figure 6. Settling matter in both lakes had significantly higher OM and lower TP concentrations compared to resuspended matter. A potential explanation for the high OM in settling material, despite the typical low chlorophyll *a* concentration of the study lakes, is the presence of large zooplankton species like *Daphnia pullicaria* and *Mixodiaptomus laciniatus* (Cruz-Pizarro & Carrillo, 1996, Villar-Argaiz et al., 2001), and greater degradation and fine mineral content of the resuspended sediments.

CONCLUDING REMARKS

The main conclusions of this work are:

- The complexity of physical, chemical, and biological processes governing P exchange at the water-sediment interface in aquatic ecosystems, expanding beyond earlier research focused solely on iron oxide redox reactions.
- Desiccation and re-flooding significantly alter sedimentary P dynamics in Sierra Nevada lakes. Desiccated sediments in both studied lakes exhibited a lower PO_4^{3-} adsorption capacity, linked to losses of amorphous Fe and Al oxides, OM, and the finest sediment fraction. These alterations stem mainly from: wind-driven removal of fine metal-oxide-rich sediment fractions and higher temperatures and oxic conditions accelerating OM mineralization.
- Observational evidence based on extensive data from La Caldera spanning over two decades (1986-2006), covering multiple drought-and-refilling (D&R) cycles, reveals the profound impact of hydrological fluctu-



	La Caldera	Río Seco
TP ($\mu g\ g^{-1}$ DW)	449	312
OM (%)	63	65

	La Caldera	Río Seco
TP ($\mu g\ g^{-1}$ DW)	820	1133
OM (%)	10	12

Figure 6. General characterization of the settling and resuspended matter in La Caldera and Río Seco. C*aracterización general del material en sedimentación y resuspendido en las lagunas de La Caldera y Río Seco.*

ations on lake dynamics. Recurrent droughts reduced lake volume and increased exposure of littoral sediments to desiccation, intensifying sediment-water interactions. TP increase markedly during drought periods due to enhanced sediment resuspension and/or deposition of P-enriched atmospheric dust, while TN showed no clear trend. While bacterial and zooplankton abundance showed no consistent trend across periods, phytoplankton and heterotrophic nanoflagellate (HNF) abundances increased during drought conditions. Long-term data indicates that lower water levels coincide with increased TP, HNF, and zooplankton abundance.

- Sedimentation and resuspension are crucial processes linking planktonic and benthic communities and regulating nutrient availability in Sierra Nevada lakes. Settling rates ranged from 0.38 to 1.18 g DW m^{-2} d^{-1}, reflecting the oligotrophy nature of lakes. The impact of resuspended material on P dynamics is lake-specific: no PO_4^{3-} increase was observed in La Caldera, whereas it significantly elevated P concentrations in Río Seco, suggesting that frequent resuspension events in the latter profoundly alter P availability.
- These findings underscore the complex biogeochemical interplay at the sediment-water interface of oligotrophic high-mountain lakes. Under projected global change, intensified WLFs are expected to strengthen benthic-pelagic coupling and profoundly reshape nutrient cycling in these sensitive ecosystems.

COMPETING INTEREST STATEMENT

The authors declare no competing interests.

AUTHOR’S CONTRIBUTION

I.d.V.: Conceptualization, Visualization, Funding-acquisition, Writing-original draft & editing; F.G.: Writing-original draft, review & editing; L.C.P.: Funding-acquisition; Writing-review.

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REFERENCES

Adrian, R., O’Reilly, C. M., Zagarese, H., Baines, S. B., Hessen, D. O., Keller, W., …. Winder, M. (2009). Lakes as sentinels of climate change. *Limnology and Oceanography*, 54, 2283-2297. DOI: 10.4319/lo.2009.54.6_part_2.2283

Alfadhel, I., Peralta-Maraver, I., Reche, I., Sánchez-Cañete, E. P., Aranda-Barranco, S., Rodríguez-Velasco, E., & Serrano-Ortiz, P. (2024). Drought conditions disrupt atmospheric carbon uptake in a Mediterranean saline lake. *Biogeosciences*, 21, 5117-5129. DOI: 10.5194/bg-21-5117-2024

Álvarez-Cobelas, M., Rojo, C., & Angeler, D. (2005). Mediterranean limnology: current status, gaps, and the future. *Journal of Limnology*, 64, 13-29. DOI: 10.4081/jlimnol.2005.13

Anderson, E. P., Marengo, J., Villalba, R., Halloy, S., Young, B., Cordero, D., Gast, F., Jaimes, E., & Ruiz, D. (2011). Consequences of climate change for ecosystems and ecosystem services in the tropical Andes (pp 1-18). In: *Climate Change and Biodiversity in the Tropical Andes*, Edited by: S. K. Herzog, R. Martínez, P. M. Jørgensen, & H. Tiessen. 348 pp. ISBN: 978-85-99875-05-6

Ardón, M., Morse, J. L., Doyle, M. W., & Bernhardt, E. S. (2010). The water quality consequences of restoring wetland hydrology to a large agricultural watershed in the southeastern coastal plain. *Ecosystems*, 13, 1060-1078. DOI: 10.1007/s10021-010-9374-x

Azorin-Molina, C., Guijarro, J. -A., McVicar, T. R., Vicente-Serrano, S. M., Chen, D., Jerez S., & Espírito-Santo, F. (2016). Trends of daily peak wind gusts in Spain and Portugal, 1961-2014. *Journal of Geophysical Research: Atmospheres*, 121, 1059-1078. DOI: 10.1002/2015JD024485

Baldwin, D. S. (1996). Effects of exposure to air and subsequent drying on the phosphate sorption characteristics of sediments from a eutrophic reservoir. *Limnology and Oceanography*, 41, 1725-1732. DOI: 10.4319/lo.1996.41.8.1725

Baldwin, D. S., & Mitchell, A. M. (2000). The effects of drying and re-flooding on the sediment and soil nutrient dynamics of lowland river-floodplain systems: a synthesis. *Regulated Rivers: Research & Management*, 16, 457-467. DOI:10.1002/1099-1646(200009/10)16:5<457::AID-RRR597>3.0.CO;2-B

Barnett, T. P., Adam, J. C., & Lettenmaier, D. P. (2005). Potential impacts of a warming climate on water availability in snow-dominated regions. *Nature*, 17, 303-309. DOI: 10.1038/nature04141

Barrow, N. J., & Shaw, T. C. (1980). Effects of drying soil in the measurement of phosphate adsorption. *Communications in Soil Science and Plant Analysis,* 11, 347-353. DOI: 10.1080/00103628009367042

Bartlett, R., & James, B. (1980). Studying dried, stored soil samples - some pitfalls. *Soil Science Society of America Journal*, 44, 721-724. DOI: 10.2136/sssaj1980.03615995004400040011x

Batzer, D. P., & Sharitz, R. R. (2006). *Ecology of freshwater and estuarine wetlands*. University of California Press. Berkeley. California. USA.

Beniston, M. (2003). Climate change in mountain regions: a review of possible impacts. *Climate Change*, 59, 5-31. DOI: 10.1023/A:1024458411589

Birch, H. F. (1960). Soil drying and soil fertility. *Tropical Agriculture (Trinidad)*, 37, 3-10.

Bloesch, J. (1982). Inshore-offshore sedimentation differences resulting from resuspension in the eastern basin of Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences*, 39, 748-759. DOI: 10.1139/f82-103

Bloesch, J. (1994). A review of methods used to measure sediment resuspension. *Hydrobiologia*, 284, 13-18. DOI: 10.1007/BF00005728

Bloesch, J. (1995). Mechanisms, measurement and importance of sediment resuspension in lakes. *Marine and Freshwater Research*, 46, 295-304. DOI: 10.1071/MF9950295

Bloesch, J. N., & Burns, M. (1980). A critical review of sedimentation traps techniques. *Schweizerische Zeitschrift fuer Hydrologie*, 42, 15-55. DOI: 10.1007/BF02502505

Boström, B., & Pettersson, K. (1982). Different patterns of phosphorus release from lake sediments in laboratory experiments. *Hydrobiologia*, 92, 415-429. DOI: 10.1007/PL00020032

Boström, B., Jansson, M., & Forsberg, C. (1982). Phosphorus release from lake sediments. In: H. Bernhardt H (ed.). *Nutrient remobilization from sediments and its limnological effects*. (pp. 5-59). E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart. Germany.

Boström, B., Andersen, J. M., Fleischer, S., & Jansson, M. (1988). Exchange of phosphorus across the sediment-water interface. *Hydrobiologia*, 170, 229-244. DOI: 10.1007/BF00024907

Brady, N. C., & Weil, R. R. (2008). *The nature and properties of soils*. Prentice-Hall. NJ. USA.

Bridgeman, T. B., Schloesser, D. W., & Krause, A. E. (2006). Recruitment of Hexagenia mayfly nymphs in western Lake Erie linked to environmental variability. *Ecological Applications*, 16, 601-611. DOI: 10.1890/1051-0761(2006)016[0601:rohmni]2.0.co;2

Bridgham, S. D., Patrick Megonigal, J., Keller, J. K., Bliss, N. B., & Trettin, C. (2006). The carbon balance of North American wetlands. *Wetlands*, 26, 889-916. DOI:10.1672/0277-5212(2006)26[889:TCBONA]2.0.CO;2

Brookes, P. C., Powlson, D. S., & Jenkinson, D. S. (1982). Measurement of microbial biomass phosphorus in soil. *Soil Biology and Biochemistry*, 14, 319-329. DOI: 10.1016/0038-

0717(82)90001-3

Bruland, G. L., & Richardson, C. J. (2006). An assessment of the phosphorus retention capacity of wetlands in the Painter Creek Watershed, Minnesota, USA. *Water, Air, and Soil Pollution*, 171, 169-184. DOI: 10.1007/s11270-005-9032-7

Cabrerizo, M. J., Medina-Sánchez, J. M., Dorado-García, I., Villar-Argaiz, M., & Carrillo, P. (2017). Rising nutrients-pulse frequency and high UVR strengthen microbial interactions. *Scientific Reports*, 7, 43615. DOI: doi.org/10.1038/srep43615

Castellano-Hinojosa, A., Tortosa, G., Fernández-Zambrano, A., Correa-Galeote, D., Bedmar, E. J., & Medina-Sánchez, J. M. (2024). Strong Saharan dust deposition events alter microbial diversity and composition in sediments of high-mountain lakes of Sierra Nevada (Spain). *Microbial Ecology*, 87, 99. DOI: 10.1007/s00248-024-02416-w

Carrillo, P., Medina-Sánchez, J. M., Villar-Argaiz, M., Bullejos, F. J., Durán, C., Bastidas-Navarro, M., ……. Modenutti, B. E. (2017). Vulnerability of mixotrophic algae to nutrient pulses and UVR in an oligotrophic southern and northern hemisphere lake. *Scientific Reports*, 7, 6333. https://doi.org/10.1038/s41598-017-06279-9

Catalan, J., Camarero, L., Felip, M., Pla-Rabes, S., Ventura, M., Buchaca, T., …… Díaz de Quijano, D. (2006). High mountain lakes: extreme habitats and witnesses of environmental change. *Limnetica*, 25, 551-584. DOI: 10.23818/limn.25.38

Clavero, V., Izquierdo, J. J., Fernández, J. A., & Niell, F. X. (1999). Influence of bacterial density on the exchange of phosphate between sediment and overlying water. *Hydrobiologia*, 392, 55-63. DOI: 10.1023/A:1003501323661

Cole, J. J., Prairie, Y. T., Caraco, N. F., McDowell, W. H., Tranvik, L. J., Striegl, R. G., ….. Melack, J. (2007). Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. *Ecosystems*, 10, 172-185. DOI: 10.1007/s10021-006-9013-8

Collins, M., Knutti, R., Arblaster, J., Dufresne, J. -L., Fichefet, T., Friedlingstein, P., …… Wehner, M. (2013). Long-term climate change: projections, commitments and irreversibility. In: T. F. Stocker, D. Qin, G. -K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley (eds.). *Climate change 2013: The Physical Science Basis.* Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. (pp. 1029-1136). Cambridge University Press, Cambridge. UK.

Cooke, G. D., Welch, E. B., Peterson, S., & Nichols, S. A. (2005). *Restoration and management of lakes and reservoirs*. CRC Press. Boca Raton. USA.

Coops, H., Beklioglu, M., & Crisman, T. J. (2003). The role of water-level fluctuations in shallow lake ecosystems - workshop conclusions. *Hydrobiologia*, 506/509, 23-27. DOI: 10.1023/B:HYDR.0000008595.14393.77

Crutzen, P. J. (2002). Geology of mankind. *Nature*, 415, 23. DOI: 10.1038/415023a

Cruz-Pizarro, L., & Carrillo, P. (1996). A high mountain oligotrophic lake (La Caldera, Sierra Nevada, Spain). In: J. J. Cruz-Sanjulián, & J. Benavente (eds.). *Wetlands: a multiapproach perspective*. (pp. 111-130). University of Granada, Granada. Spain.

Darke, A. K., & Walbridge, M. R. (2000). Al and Fe biogeochemistry in a floodplain forest: implications for P retention. *Biogeochemistry*, 51, 1-32. DOI: 10.1023/A:1006302600347

De Groot, C. J. (1991). The influence of FeS on the inorganic phosphate system in sediments. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie,* 24, 3029-3035. DOI: 10.1080/03680770.1989.11899224

De Groot, C. J., & Fabre, A. C. (1993). The impact of desiccation of a freshwater marsh (Garcines Nord, Camargue, France) on the sediment-water-vegetation interactions. Part 3: the fractional composition and the phosphate adsorption characteristics of the sediment. *Hydrobiologia*, 252, 105-116. DOI: 10.1007/BF00000132

De Groot, C. J., & Golterman, H. L. (1993). On the presence of organic phosphate in some Camargue sediments: evidence for the importance of phytate. *Hydrobiologia*, 252, 117-126. DOI: 10.1007/BF00000133

De Groot, C. J., & VanWijck, C. (1993). The impact of desiccation of a freshwatermarsh (Garcines Nord, Camarge, France) on sediment water–vegetation interactions. Part 1: the sediment chemistry. *Hydrobiologia*, 252, 83-94. DOI: 10.1007/BF00000130

de Vicente, I. (2004). Intercambio de nutrientes en la interfase agua-sedimento de dos lagunas costeras de elevado nivel trófico: la Albufera de Adra (Almería). (PhD. Tesis. Universidad de Granada, España). Retrieved: https://digibug.ugr.es/handle/10481/56391?show=full

de Vicente, I. (2021). Biogeochemistry of mediterranean wetlands: a review about the effects of water-level fluctuations on phosphorus cycling and greenhouse gas emissions. *Water*, 13, 1510. DOI: 10.3390/w13111510

de Vicente, I., Serrano, L., Amores, V., Clavero, V., Cruz-Pizarro, L. (2003). Sediment phosphate fractionation and interstitial water phosphate concentration in two coastal lagoons (Albuferas de Adra, SE Spain). *Hydrobiologia*, 492, 95-105. DOI: 10.1023/A:1024813811763

de Vicente, I., Amores, V., Escot, C., Basanta, A., & Cruz-Pizarro, L. (2005). Temporal and spatial trends in the sedimentation process in a canyon-type reservoir (El Gergal, Seville, Spain). *Archiv für Hydrobiologie*, 163, 241-257. DOI: 10.1127/0003-9136/2005/0163-0241

de Vicente, I., Huang, P., Andersen, F. Ø., & Jensen, H. S. (2008a). Phosphate adsorption by fresh and aged aluminium hydroxide. Consequences for lake restoration. *Environmental Science and Technology*, 42, 6650-6655. DOI: 10.1021/es800503s

de Vicente, I., Rueda, F., Cruz-Pizarro, L., & Morales-Baquero, R. (2008b). Implications of seston settling on phosphorus dynamics in three reservoirs of contrasting trophic state. *Fundamental and Applied Limnology*, 170, 263-272. DOI: 10.1127/1863-9135/2008/0170-0263

de Vicente, I., Ortega-Retuerta, E., Romera, O., Morales-Baquero, R., & Reche, I. (2009). Contribution of transparent exopolymer particles to carbon sinking flux in an oligotrophic reservoir. *Biogeochemistry*, 96, 13-23. DOI: 10.1007/s10533-009-9342-8

de Vicente, I., Andersen, F. Ø., Hansen, H. C. B., Cruz-Pizarro, L., & Jensen, H. S. (2010a). Water level fluctuations may decrease phosphate adsorption capacity of the sediment in oligotrophic high mountain lakes. *Hydrobiologia*, 651, 253-264. DOI: 10.1007/s10750-010-0304-x

de Vicente, I., Guerrero, F., Jiménez-Gómez, F., & Cruz-Pizarro, L. (2010b). Settling and resuspended particles: A source or a sink of phosphate in two contrasting oligotrophic high mountain lakes? *Comptes Rendus Geoscience*, 342, 46-52. DOI: 10.1016/j.crte.2009.10.004

de Vicente, I., Cruz-Pizarro, L., & Rueda, F. (2010c). Sediment resuspension in two adjacent shallow coastal lakes: controlling factors and consequences on phosphate dynamics. *Aquatic Sciences*, 72, 21-31. DOI: 10.1007/s00027-009-0107-1

de Vicente, I., López, R., Pozo, I., & Green, A. (2012). Nutrient and sediment dynamics in a Mediterranean shallow lake in southwest Spain. *Limnetica*, 31, 231-250. DOI: 10.23818/limn.31.21

de Vicente, I., García-Bermúdez, A., & Cruz-Pizarro, L. (2022). Estado trófico y características morfométricas como factores reguladores de las tasas de sedimentación en embalses mediterráneos. *Ingeniería del Agua*, 26, 173-183. DOI: 10.4995/ia.2022.17609

Dommergues, Y., & Mangenot, F. (1970). *Ecologie microbienne dusol*. Masson. Paris. France.

EEA. (2025). E*urope's environment and climate: knowledge for resilience, prosperity and sustainability*. DOI: 10.2800/3817344

Einsele, W. (1936). Über die Beziehungen des Eisenkreislaufs zum Phosphatkreislauf im eutrophen See. A*rchiv für Hydrobiologie*, 29, 664-686.

Einsele, W. (1938). Über Chemische and Kolloidchemische Vorgänge in Eisen-Phosphat-Systemen unter limnochemische und limnogeologischen Gesichtspunkten. *Archiv für Hydrobiologie*, 33, 361-387.

Estrela, T. (2006). La gestión de las sequías en España. *Ingeniería y Territorio*, 74, 52-57.

Fabre, A. (1988). Experimental studies on some factors influencing phosphorus solubilization in connexion with the drawdown of a reservoir. *Hydrobiologia*, 159, 153-158. DOI:

10.1007/BF00014723

Fennessy, M. S., Wardrop, D. H., Moon, J. B., Wilson, S., & Craft, C. (2017). Soil carbon sequestration in freshwater wetlands varies across a gradient of ecological condition and by ecoregion. *Ecological Engineering*, 114, 129-136. DOI: 10.1016/j.ecoleng.2017.09.013

Froelich, P. N. (1988). Kinetic control of dissolved phosphate in natural rivers and estuaries: a primer on the phosphate buffer mechanism. *Limnology and Oceanography*, 33, 649-668. DOI: 10.4319/lo.1988.33.4part2.0649

Gálvez, J. A., Niell, F. X., & Lucena, J. (1991). C:N:P ratio of settling seston in a eutrophic reservoir. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 24, 1390-1395. DOI: 10.1080/03680770.1989.11898988

Gálvez, J. A., & Niell, F. X. (1993). Sedimentation and mineralization of seston in a eutrophic reservoir, with a tentative sedimentation model. In: M. Straškraba, J. G. Tundisi, & A. Duncan (eds.). *Comparative reservoir limnology and water quality management.* Developments in Hydrobiology, vol 77. (pp. 119-126). Springer, Dordrecht. Germany. DOI: 10.1007/978-94-017-1096-1_7

García-Jurado, F., Jiménez-Gómez, F., & Guerrero, F. (2011). Effects of a dry period on the limnological characteristics of a Mediterranean high mountain lake. *Limnetica*, 30, 5-16. DOI: 10.23818/limn.30.02

García-Jurado, F., de Vicente, I., Galotti, A., Reul, A., Jiménez-Gómez, F., & Guerrero, F. (2012). Effect of drought conditions on plankton community and on nutrient availability in an oligotrophic high mountain lake. *Arctic, Antarctic and Alpine Research*, 44, 50-61. DOI: 10.1657/1938-4246-44.1.50

Gardner, W. D. (1977). Fluxes, dynamics and chemistry of particulates in the ocean. (PhD. Thesis. Woods Hole Oceanographic Institute, USA). Retrieved: https://apps.dtic.mil/sti/tr/pdf/ADA058770.pdf

Gilbert, J. D., Guerrero, F., & de Vicente, I. (2014). Sediment desiccation as a driver of phosphate availability in the water column of Mediterranean wetlands. *Science of the Total Environment*, 466-467, 965-975. DOI: 10.1016/j.scitotenv.2013.07.123

Golterman, H. L. (1984). Sediments, modifying and equilibrating factors in the chemistry of freshwater. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 22, 23-59. DOI: 10.1080/03680770.1983.11897265

Golterman, H. L. (1990). Some aspects of nutrients cycles in the Camarge (France). *Scientia Gerundensis*, 16, 11-17.

Golterman, H. L. (1996). Fractionation of sediment phosphate with chelating compounds: a simplification and a comparison with other methods. *Hydrobiologia*, 335, 87-95. DOI: 10.1007/BF00013687

Golterman, H. L. (1998). The distribution of phosphate over iron-bound and calcium-bound phosphate in stratified sediments. *Hydrobiologia*, 364, 75-81. DOI: 10.1023/A:1003159924052

Golterman, H. L. (2001). Phosphate release from anoxic sediments or “what did Mortimer really write?”. *Hydrobiologia*, 450, 99-106. DOI: 10.1023/A:1017559903404

Golterman, H. L. (2004). *The chemistry of phosphate and nitrogen compounds in sediments.* Springer. Dordrecht. Germany.

Golterman, H. L., & Booman, A. (1988). Sequential extraction of iron-phosphate and calcium phosphate by chelating agents. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 23, 904-909. DOI: 10.1080/03680770.1987.11899738

González-Olalla, J. M., Medina-Sánchez, J. M., Lozano, I. L., Villar-Argaiz, M., & Carrillo, P. (2018). Climate-driven shifts in algal-bacterial interaction of high-mountain lakes in two years spanning a decade. *Scientific Reports*, 8, 10278. DOI: 10.1038/s41598-018-28543-2

Guerrero, F. (2021). Advances in mountain and Mediterranean wetlands conservation. *Water*, 2021, 13, 1953. DOI: 10.3390/w13141953

Hamilton, S. K., Bruesewitz, D. A., Horst, G. P., Weed, D. B., & Sarnelle, O. (2009). Biogenic calcite-phosphorus precipitation as a negative feedback to lake eutrophication. *Canadian Journal of Fisheries and Aquatic Sciences*, 66, 343-350. DOI: 10.1139/F09-00

Havens, K., & Jeppesen, E. (2018). Ecological responses of lakes to climate change. *Water*, 2018, 10, 917. DOI: 10.3390/w10070917

Haynes, R. J., & Swift, R. S. (1985). Effects of air-drying on the adsorption and desorption of phosphate and levels of extractable phosphate in a group of New Zealand acid soils. *Geoderma*, 35, 145-157. DOI: 10.1016/0016-7061(85)90027-8

Hem, J. D., & Roberson, C. E. (1967). *Form and stability of aluminium hydroxide complexes in dilute solution*. U.S. Geological Survey Water-Supply Paper 1827-A.

Hessen, D. O., Andersen, T., McKay, D. A., Kosten, S., Meerhoff, M., Pickard, A., & Spears, B. M. (2024). Lake ecosystem tipping points and climate feedbacks. *Earth System Dynamics*, 15, 653-669. DOI: 10.5194/esd-15-653-2024, 2024

Hirsch, P. E., Schillinger, S., Weigt, H., & Burkhardt-Holm, P. (2014). A hydro-economic model for water level fluctuations: combining limnology with economics for sustainable development of hydropower. *PLOS One*, 9, e114889. DOI:10. 1371/journal.pone.0114889

IPCC (2021). Climate Change 2021: The physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change. In: *V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, N. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou (eds.)*. (pp. 1-2391). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. DOI:10.1017/9781009157896.

Istvánovics, V., Honti, M., Torma, P., & Kousal, J. (2022). Record-setting algal bloom in polymictic Lake Balaton (Hungary): a synergistic impact of climate change and (mis)management. *Freshwater Biology*, 67, 1091-1106. DOI: 10.1111/fwb.13903

Jernelöv, A. (1971). Phosphate reduction in lakes by precipitation by aluminium sulphate. 5th International Water Pollution Research Conference. Pergamon Press. New York. USA.

Jiménez, L., Rühland, K. M., Jeziorski, A., Smol, J. P., & Pérez-Martínez, C. (2018). Climate change and Saharan dust drive recent cladoceran and primary production changes in remote alpine lakes of Sierra Nevada, Spain. *Global Change Biology*, 2018, 24, e139-e158. DOI: 10.1111/gcb.13878

Jones, L., Gorst, A., Elliott, J., Fitch, A., Illman, H., Evans, C., … Smale, R. (2020). *Climate driven threshold effects in the natural environment*. Report to the Climate Change Committee. May 2020.

Kadlec, R. H., & Wallace, S. D. (2009). *Treatment wetlands*. CRC Press. Boca Raton. USA.

Kalff, J. (2002). *Limnology: inland water ecosystems.* Prentice Hall. NJ. USA.

Kinsman-Costello, L. (2012). Effects of water level fluctuations on phosphorus, iron, sulfur, and nitrogen cycling in shallow freshwater ecosystems. (PhD. Thesis. Michigan State University, USA). Retrieved: https://d.lib.msu.edu/etd/242

Kinsman-Costello, L. E., O'Brien, J., & Hamilton, S. K. (2014). Re-flooding a historically drained wetland leads to rapid sediment phosphorus release. *Ecosystems*, 17, 641-656. DOI: 10.1007/s10021-014-9748-6

Kleeberg, A. (2002). Phosphorus sedimentation in seasonal anoxic Lake Scharmützel, NE Germany. *Hydrobiologia*, 472, 53-65. DOI: 10.1023/A:1016356714276

Kodama, H., & Schnitzer, M. (1977). Effect of fulvic acid on crystallization of Fe (III) oxides. *Geoderma*, 19, 279-291. DOI: 10.1016/0016-7061(77)90070-2

Kodama, H., & Schnitzer, M. (1980). Effect of fulvic acid on the crystallization of aluminium hydroxides. *Geoderma*, 24, 195-205. DOI: 10.1016/0016-7061(80)90023-3

Kopáček, J., Hejzlar, J., Porcal, P., & Stuchlík, E. (2011). Phosphorus loading of mountain lakes: Terrestrial export and atmospheric deposition. *Limnology and Oceanography*, 56, 1343-1354. DOI: 10.4319/lo.2011.56.4.1343

Kristensen, P., Søndergaard, M., & Jeppesen, E. (1992). Resuspension in a shallow eutrophic lake. *Hydrobiologia*, 228, 101-109. DOI: 10.1007/BF00006481

Lijklema, L. (1980). Interaction of orthophosphate with iron (III) and aluminium hydroxides. *Environmental Science and Technology*, 14, 537-540. DOI: 10.1021/es60165a013

Llamas, M. R. (1997). Consideraciones sobre la sequía de 1991 a 1995 en España. *Ingeniería del Agua*, 4, 39-50. DOI: 10.4995/ia.1997.2714

López, P. (1991). Sedimentary phosphorus dynamics in epicontinental systems: a literature review. *Oecologia Aquatica*, 10, 113-125.

Marsh, P., & Lesack, L. F. W. (1996). The hydrologic regime of perched lakes in the Mackenzie Delta: potential responses to climate change. *Limnology and Oceanography*, 41, 849-856. DOI: 10.4319/lo.1996.41.5.0849

Medina-Sánchez, J. M., Villar-Argaiz, M., Sánchez-Castillo, P., Cruz-Pizarro, L., & Carrillo, P. (1999). Structure changes in a planktonic food web: biotic and abiotic controls. *Journal of Limnology*, 58, 213-222. DOI: 10.4081/jlimnol.1999.213

Medina-Sánchez, J. M., Cabrerizo M. J., González-Olalla, J. M., Villar-Argaiz, M., & Carrillo, P. (2022). High mountain lakes as remote sensors of global change. In: R. Zamora, & M. Oliva (eds.). *The landscape of the Sierra Nevada* (pp 261-278). Springer, Berlin. Germany. DOI: 10.1007/978-3-030-94219-9_16

Mesman, J. P., Stelzer, J. A. A., Dakos, V., Goyette, S., Jones, I. D., Kasparian, J., ….. Ibelings, B. W. (2021). The role of internal feedbacks in shifting deep lake mixing regimes under a warming climate. *Freshwater Biology*, 66, 1021-1035. DOI: 10.1111/fwb.13704

Middleton, N.J., & Goudie, A. S. (2001). Saharan dust: sources and trajectories. *Transactions of the Institute of British Geographers*, 26, 165-181. DOI: 10.1111/1475-5661.00013

Milly, P. C. D., Dunne, K. A., & Vecchia, A. (2005). Global pattern of trends in streamflow and water availability in a changing climate. *Nature*, 438, 347-350. DOI: 10.1038/nature04312

Morales-Baquero, R., Carrillo, P., Reche, I. & Sánchez-Castillo, P. (1999). Nitrogen-phosphorus relationship in high mountain lakes: effects of the size of catchment basins. *Canadian Journal of Fisheries and Aquatic Sciences*, 56, 1809-1817. DOI: 10.1139/f99-130

Morales-Baquero, R., Pulido-Villena, E., & Reche, I. (2006). Atmospheric inputs of phosphorus and nitrogen to the southwest Mediterranean region: biogeochemical responses of high mountain lakes. *Limnology and Oceanography*, 51, 830-837. DOI: 10.4319/lo.2006.51.2.0830

Morales-Baquero, R., Pulido-Villena, E., & Reche, I. (2013). Chemical signature of Saharan dust on dry and wet atmospheric deposition in the south-western Mediterranean region. *Tellus B: Chemical and Physical Meteorology*, 65, 18720. DOI: 10.3402/tellusb.v65i0.18720

Mortimer, C. H. (1941). The exchange of dissolved substances between mud and water in lakes. *Journal of Ecology*, 29, 280-329. DOI: 10.2307/2256395

Mortimer, C. H. (1971). Chemical exchanges between sediments and water in the Great Lakes - speculations on probable regulatory mechanisms. *Limnology and Oceanography*, 16, 387-404. DOI: 10.4319/lo.1971.16.2.0387

Novak, J. M., & Watts, D. W. (2006). Phosphorus sorption by sediments in southeastern coastal plain in-stream wetland. *Journal of Environmental Quality*, 35, 1975-1982. DOI: 10.2134/jeq2006.0077

Pardo, P., López Sánchez, J. F., Rauret, G., Ruban V., Muntau, H., & Quevauiller, Ph. (1999). Study of the stability of extractable phosphate concentration in a candidate reference material using a modified Williams extraction procedure. *Analyst*, 124, 407-411. DOI: 10.1039/A808693A

Pérez-Martínez, C., Conde-Porcuna, J. M., Ramos-Rodríguez, E., Moreno, E., Rühland, K. M., Jeziorski, ….. Jiménez, L. (2022). Paleolimnological indicators of global change. In: R. Zamora, & M. Oliva (eds.), *The landscape of the Sierra Nevada* (pp. 279-291). Springer, Berlin. Germany. DOI: 10.1007/978-3-030-94219-9_17

Peters, R. H., & Cattaneo, A. (1984). The effects of turbulence on phosphorus supply in a shallow bay of Lake Memphremagog. V*erhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 22, 185-189. DOI: 10.1080/03680770.1983.11897286

Prairie, Y., de Montigny, C., & Giorgio, P. (2001). Anaerobic phosphorus release from sediments: a paradigm revisited. *Verhandlungen der Internationalen Vereinigung für Theoretische* *und Angewandte Limnologie*, 27, 4013-4020. DOI: 10.1080/03680770.1998.11901750

Pulido-Villena, E., Ortega-Retuerta, E., Morales-Baquero, R., & Reche, I. (2003). El papel de la escala en los patrones de variación del bacterioplancton en lagunas de alta montaña. *Limnetica*, 22, 183-193. DOI: 10.23818/limn.22.12

Qiu, S., & McComb, A. J. (2002). Interrelations between iron extractability and phosphate sorption in reflooded airdried sediments. *Hydrobiologia*, 472, 39-44. DOI: 10.1023/A:1016317100164

Reche, I., Pulido-Villena, E., Conde-Porcuna, J. M., & Carrillo, P. (2001). Photoreactivity of dissolved organic matter from high-mountain lakes of Sierra Nevada, Spain. *Arctic Antarctic and Alpine Research*, 33, 426-434. DOI: 10.1080/15230430.2001.12003451

Reche, I., Mladenov, N., Pulido-Villena, E., & Morales-Baquero, R. (2022). Atmospheric inputs and biogeochemical consequences in high-mountain lakes. In: R. Zamora, & M. Oliva (eds.). *The landscape of the Sierra Nevada* (pp. 293-306). Springer, Berlin. Germany. DOI: 10.1007/978-3-030-94219-9_18

Reddy, K. R., & DeLaune, R. D. (2008). *Biogeochemistry of wetlands*. Science and Applications. CRC Press. Boca Raton. USA.

Reddy, K. R., Fisher, M. M., & Ivanoff, D. (1996). Resuspension and diffusive flux of nitrogen and phosphorus in a hypereutrophic lake. *Journal of Environmental Quality*, 25, 363-371. DOI: 10.2134/jeq1996.00472425002500020022x

Reddy, K. R., DÁngelo, E. M., & Harris, W. G. (2000). Biogeochemistry of wetlands. In: M. E. Sumer (ed.). *Handbook of Soil Science*. (pp. 89-119). CRC Press, Boca Raton, USA.

Reitzel, K., Hansen, J., Andersen, F. Ø., Hansen, K. H., & Jensen, H. S. (2005). Lake restoration by dosing aluminium relative to mobile phosphorus in the sediment. *Environmental Science and Technology*, 39, 4134-4140. DOI: 10.1021/es0485964

Ren, S., Zhang, B., Wang, W. -J., Yuan, Y., & Guo, Ch. (2021). Sedimentation and its response to management strategies of the Three Gorges Reservoir, Yangtze River, China. *Catena*, 199, 105096. DOI: 10.1016/j.catena.2020.105096

Richardson, J., Miller, C., Maberly, S. C., Taylor, P., Globevnik, L., Hunter, P., …… Carvalho, L. (2018). Effects of multiple stressors on cyanobacteria abundance vary with lake type. *Global Change Biology Bioenergy*, 24, 5044-5055. DOI: 10.1111/gcb.14396

Richardson, K., Steffen, W., Lucht, W., Bendtsen, J., Cornell, S. E., Donges, J. F., ……. Rockström, J. (2023). Earth beyond six of nine planetary boundaries. *Science Advances*, 9, 37, eadh2458. DOI: 10.1126/sciadv.adh24

Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin III, F. S., Lambin, E. F., ….. Foley, J. A. (2009). A safe operating space for humanity. *Nature*, 461, 472-475. DOI: 10.1038/461472a

Rothe, M., Kleeberg, A., Grüneberg, B., Friese, K., Pérez Mayo, M., & Hupfer, M. (2015). Sedimentary sulphur:iron ratio indicates vivianite occurrence: a study from two contrasting freshwater systems. *PLOS One*, 10, e0143737. DOI: 10.1371/journal.pone.0143737

Rothe, M., Kleeberg, A., & Hupfer, M. (2016). The occurrence, identification and environmental relevance of vivianite in waterlogged soils and aquatic sediments. *Earth-Science Reviews*, 158, 51-64. DOI: 10.1016/j.earscirev.2016.04.008

Ryding, S. -O., & Forsberg, C. (1977). Sediments as a nutrient source in shallow polluted lakes: In: H. L. Golterman (ed.). *Interactions between sediment and water*. (pp. 227-234). Dr. W. Junk, The Hague, The Netherlands.

Rydin, E., & Welch, E. B. (1998). Aluminium dose required to inactivate phosphate in lake sediments. *Water Research*, 32, 2969-2976. DOI: 10.1016/S0043-1354(98)00055-4

Saar, K., Nõges, P., Søndergaard, M., Jensen, M., Jørgensen, C., Reitzel, K., …. Jensen, H. S. (2022). The impact of climate change and eutrophication on phosphorus forms in sediment: results from a long-term lake mesocosm experiment. *Science of the Total Environment*, 825, 153751. DOI: 10.1016/j.scitotenv.2022.153751

Sah, R. N., & Mikkelsen, D. S. (1989). Phosphorus behavior in flooded-drained soils. I. Effects on phosphorus sorption. *Soil Science Society of America Journal*, 53, 1718-1722. DOI:

10.2136/sssaj1989.03615995005300060018x

Selig, U. (2003). Particle size-related phosphate binding and P-release at the sediment -water interface in a shallow German lake. *Hydrobiologia*, 492, 107-118. DOI: 10.1023/A:1024865828601

Schwertmann, U. (1966). Inhibitory effect of soil organic matter on the crystallization of amorphous ferric hydroxide. *Nature*, 212, 645-646. DOI: 10.1038/212645b0

Slomp, C. P., Mort, H. P., Jilbert, T., Reed, D. C., Gustafsson, B. G., & Wolthers, M. (2013). Coupled dynamics of iron and phosphorus in sediments of an oligotrophic coastal basin and the impact of anaerobic oxidation of methane. *PLOS One*, 8, e62386. DOI: 10.1371/journal.pone.0062386

Sommaruga, R. (2015). When glaciers and ice sheets melt: consequences for planktonic organisms. *Journal of Plankton Research*, 37, 509-518. DOI: 10.1093/plankt/fbv027

Søndergaard, M. (1993). Organic carbon pools in two Danish lakes: flow of carbon to bacterioplankton. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 25, 593-598. DOI: 10.1080/03680770.1992.11900196

Søndergaard, M., Kristensen, P., & Jeppesen, E. (1992). Phosphorus release from resuspended sediment in the shallow and wind exposed Lake Arresø, Denmark. *Hydrobiologia*, 228, 91-99. DOI: 10.1007/BF00006480

Søndergaard, M., Nielsen, A., Skov, C., Baktoft, H., Reitzel, K., Kragh, T., & Davidson, T. A. (2023). Temporarily and frequently occurring summer stratification and its effects on nutrient dynamics, greenhouse gas emission and fish habitat use: case study from Lake Ormstrup (Denmark). *Hydrobiologia*, 850, 65-79. DOI: 10.1007/s10750-022-05039-9

Sparling, G. P., Whale, K. N., & Ramsay, A. J. (1985). Quantifying the contribution from the soil microbial biomass to the extractable P levels of fresh and air-dried soils. Australian *Journal of Soil Research*, 23, 613-621. DOI: 10.1071/sr9850613

Spears, B. M., Chapman, D. S., Carvalho, L., Feld, C. K., Gessner, M. O., Piggott, J. J., …. Birk, S. (2021). Making waves. Bridging theory and practice towards multiple stressor management in freshwater ecosystems. *Water Research*, 196, 116981. DOI: 10.1016/j.watres.2021.116981

Steffen, W., Persson, Å., Deutsch, L., Zalasiewicz, J., Williams, M., Richardson, K., ….. Svedin, U. (2011). The Anthropocene: from global change to planetary stewardship. *Ambio*, 40, 739-761. DOI: 10.1007/s13280-011-0185-x

Steffen, W., Broadgate, W., Deutsch, L., Gaffney, O., & Ludwig, C. (2015a). The trajectory of the Anthropocene: the great acceleration. *The Anthropocene Review*, 2, 81-98. DOI: 10.1177/2053019614564785

Steffen, W., Richardson, K., Rockström, J., Cornell, S. E., Fetzer, I., Bennett, E. M., …. Sörlin, S. (2015b). Planetary boundaries: guiding human development on a changing planet. *Science*, 347, 1259855. DOI: 10.1126/science.1259855

Stumm, W., & Morgan, J. J. (1970). *Aquatic chemistry*. Wiley-Interscience. New York. USA.

Sumi, T. (2018). Reservoir sedimentation and sustainable development. In: *26th ICOLD Congress*, July 1-7. GR. Q100, Vienna, Austria.

Tammeorg, O., Chorus, I., Spears, B., Nõges, P., Nürnberg, G. K., Tammeorg, P., …. Lürling, M. (2024). Sustainable lake restoration: from challenges to solutions. *WIREs Water*, 2024, 11, e1689. DOI: 10.1002/wat2.1689

Tartari, G., & Biasci, G. (1997). Trophic status and lake sedimentation fluxes. *Water, Air, and Soil Pollution*, 99, 523-531. DOI: 10.1007/978-94-011-5552-6_54

Turner, M. A., Huebert, D. B., Findlay, D. L., Hendzel, L. L., Bodaly, R. A., Jansen, W. A., …. Kasian, S. E. M. (2005). Divergent impacts of experimental lake-level drawdown on planktonic and benthic plant communities in a boreal forest lake. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 991-1003. DOI: 10.1139/f05-003

Twinch, A. J. (1987). Phosphate exchange characteristics of wet and dried sediment samples from a hypertrophic reservoir: implications for the measurements of sediment phosphorus status. *Water Research*, 21, 1225-1230. DOI: 10.1016/0043-1354(87)90174-6

Tito, R., Vasconcelos, H. L., & Feeley, K. J. (2020). Mountain ecosystems as natural laboratories for climate changes experiments. *Frontiers in Forest and Global Change*, 3, 38. DOI: 10.3389/ffgc.2020.00038

van Kuppevelt, V., Reitzel, K., & Hupfer, M. (2025). Vivianite as a phosphorus source in lake sediments: importance of increased sulphate reduction on phosphorus mobilisation. *Journal of Soils and Sediments*, 25, 1406-1421. DOI: 10.1007/s11368-025-03986-z

Villar-Argaiz, M., Medina-Sánchez, J. M., Cruz-Pizarro, L., & Carrillo, P. (2001). Inter- and intra-annual variability in the phytoplankton community of a high mountain lake: the influence of external (atmospheric) and internal (recycled) sources of phosphorus. *Freshwater Biology*, 46, 1017-1034. DOI: 10.1046/j.1365-2427.2001.00734.x

Villar-Argaiz, M., Medina-Sánchez, J. M., & Carrillo, P. (2002a). Microbial plankton response to contrasting climatic conditions: insights from community structure, productivity and fraction stoichiometry. *Aquatic Microbial Ecology*, 29, 253-266. DOI: 10.3354/ame

Villar-Argaiz, M., Medina-Sánchez, J. M., & Carrillo, P. (2002b). Interannual changes in the C.N.P ratios of seston and zooplankton of a high mountain lake in Sierra Nevada, Spain. *Water, Air and Soil Pollution: Focus*, 2, 359-378. DOI: 10.1023/A:1020135515647

Vuillemin, A., Friese, A., Wirt, R., Schuessler, J. A., Schleicher, A. M., Kemnitz, H., ….. the Towuti Drilling Project Science team. (2020). Vivianite formation in ferruginous sediments from Lake Towuti, Indonesia. *Biogeosciences*, 17, 1955-1973. DOI: 10.5194/bg-17-1955-2020

Water Framework Directive (2000). Directive 2000/60/EC of the European Parliament and of the council of 23rd October 2000 establishing a framework for community action in the field of water policy. *Official Journal of the European Communities*, L327.

Welch, E. B., & Cooke, G. D. (1999). Effectiveness and longevity of phosphorus inactivation with alum. *Lake and Reservoir Management*, 15, 5-27. DOI: 10.1080/07438149909353948

Weyhenmeyer, G. A., & Bloesch, J. (2001). The pattern of particle flux variability in Swedish and Swiss lakes. *Science of the Total Environment*, 266, 69-79. DOI: 10.1016/S0048-9697(00)00739-7

Weyhenmeyer, G. A., Meili, M., & Pierson, D. C. (1995). A simple method to quantify sources of settling particles in lakes: resuspension versus new sedimentation of material from planktonic production. *Marine and Freshwater Research*, 46, 223-231. DOI: 10.1071/MF9950223

Wilson, J. S., &. Baldwin, D. S. (2008). Exploring the “Birch effect” in reservoir sediments: influence of inundation history on aerobic nutrient release. *Chemistry and Ecology*, 24, 379-386. DOI: 10.1080/02757540802497582

Williams, J. D. H., Syers, J. K., Shukla, S. S., Harris, R. F., & Armstrong, D. E. (1971). Levels of inorganic and total phosphorus in lake sediments as related to other sediment parameters. *Environmental Science and Technology*, 5, 1113-1120. DOI: 10.1021/es60058a001

White, M. S., Xenopoulos, M. A., Hogsden, K. L., Metcalfe, R.A., & Dillon, P. J. (2008). Natural lake level fluctuations and associated concordance with water quality and aquatic communities within small lakes of the Laurentian Great Lakes. *Hydrobiologia*, 613, 21-31. DOI: 10.1007/s10750-008-9469-y

Wong, S. W., Barry, M. J., Aldous, A. R., Rudd, N. T., Hendrixson, H. A, & Doehring, C. M. (2011). Nutrient release from a recently flooded delta wetland: comparison of field measurements to laboratory results. *Wetlands*, 31, 433-443. DOI: 10.1007/s13157-010-0137-4

Woolway, R. I., & Merchant, C. J. (2019). Worldwide alteration of lake mixing regimes in response to climate change. *Nature Geoscience*, 12, 271-276. DOI: 10.1038/s41561-019-0322-x

Woolway, R. I., Kraemer, B. M., Lenters, J. D., Merchant, C. J., O’Reilly, C. M., & Sharma, S. (2020). Global lake responses to climate change. *Nature Reviews Earth and Environments*, 1, 388-403. DOI: 10.1038/s43017-020-0067-5

Woolway, R. I., Sharma, S., Weyhenmeyer, G.

A., Debolskiy, A., Golub, M., Bettín, D. M., …. Jennings, E. (2021). Phenological shifts in lake stratification under climate change. *Nature Communications*, 12, 2318. DOI: 10.1038/s41467-021-22657-4

Yao, Z., Zhang, L., Tang, S, Li, X., & Hao, T., (2017). The basic characteristics and spatial patterns of global cultivated land change since the 1980s. *Journal of Geographical Sciences*, 27(7): 771-785. DOI:10.1007/s11442-017-1405-5

Yu, J., Zhang, Y., Zhong, J., Ding, H., Zheng, X., Wang, Z., & Zhang, Y. (2020). Water-level alterations modified nitrogen cycling across sediment-water interface in the Three Gorges Reservoir. *Environmental Science and Pollution Research*, 27, 25886-25898. DOI: 10.1007/s11356-019-06656-z

Zamora R., Lorite, J., Matías, L., Leverkus, A. B., Jimenez, M., Medina-Sánchez, J. M., …. Reche, I. (2022). Concluding notes: ecosystems of Sierra Nevada in the Anthropocene: a new cocktail of species and ecological interactions. In: R. Zamora, & M. Oliva (eds.). *The landscape of the Sierra Nevada*. (pp. 307-310). Springer, Berlin. Germany.

Zhang, Y., Lin, X., & Werner, W. (2003). The effect of soil flooding on the transformation of Fe oxides and the adsorption/desorption behavior of phosphate. *Journal of Plant Nutrition and Soil Science*, 166, 68-75. DOI: 10.1002/jpln.200390014

Zedler, J. B. (2003). Wetlands at your service: reducing impacts of agriculture at the watershed scale. *Frontiers in Ecology and the Environment*, 1, 65-72. DOI: 10.1890/1540-9295(2003)001[0065:WAYSRI]2.0.CO;2s