











Food web structure, biodiversity and trophic interactions in Sierra Nevada high-mountain lakes

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ABSTRACT

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The food web in the fishless lakes of Sierra Nevada is largely shaped by several environmental factors, primarily depth and morphometry. Over the past 50 years, numerous studies have explored the trophic compartments of these ecosystems, with a primary focus on the taxonomy and ecology of planktonic species and coleopterans. This paper synthesizes research in these areas. In terms of taxonomy, several species have been recorded for the first time worldwide, such as the chrysophyte *Chromulina nevadensis*. Other plankton species have been newly documented in Spain, including the diatom *Achnanthydium macrocephalum* and the rotifer *Trichocerca relictata*, while *Daphnia* cf. *pulex* have been reported for the first time in European high mountain lakes. Ecological research has also focused on biodiversity, life history strategies, stoichiometry and trophic interactions. Key findings include: (i) low species richness and the Shannon-Wiener diversity in planktonic communities; (ii) temperature and mineralization as likely primary drivers of zooplankton composition; (iii) evidence supporting the concept of rheostasis in zooplankton; (iv) pioneering insights into links between organismal stoichiometry and life-history strategies; (v) broad trophic niches in dytiscid beetles, which primarily feed on zooplankton; (vi) discovery of a mutualistic relationship between an epibiont green algae and *Daphnia*; and (vii) the significant role of multiple interacting environmental factors on the algae-bacteria relationship.

KEY WORDS: phytoplankton, zooplankton, bacterioplankton, coleoptera, stoichiometry.

RESUMEN

Estructura de la red alimenticia, biodiversidad e interacciones tróficas en lagunas de alta montaña de Sierra Nevada

La red trófica en las lagunas sin peces de Sierra Nevada está fuertemente condicionada por distintos factores ambientales, principalmente la profundidad y la morfometría. Durante los últimos 50 años, numerosos estudios han explorado los compartimentos tróficos de estos ecosistemas, con un enfoque principal en la taxonomía y la ecología de las especies planctónicas y de los coleópteros. Este trabajo sintetiza la investigación en estas áreas. En cuanto a la taxonomía, se han registrado varias especies por primera vez a nivel mundial, como la crisofita *Chromulina nevadensis*. Otras especies planctónicas han sido documentadas por primera vez en España, entre ellas la diatomea *Achnanthydium macrocephalum* y el rotífero *Trichocerca relictata*, mientras que *Daphnia* cf. *pulex* se ha citado por primera vez en sistemas lacustres de alta montaña europeos. Las investigaciones eco-

lógicas también se han centrado en la biodiversidad, las estrategias de vida, la estequiometría y las interacciones tróficas. Los principales hallazgos incluyen: (i) baja riqueza de especies y diversidad de Shannon-Wiener en las comunidades planctónicas; (ii) identificación de la temperatura y la mineralización como probablemente los principales factores que controlan la composición del zooplancton; (iii) evidencias que respaldan el concepto de reostasis en el zooplancton; (iv) perspectivas pioneras sobre las relaciones entre la estequiometría de los organismos y las estrategias de historia de vida; (v) nichos tróficos en los coleópteros ditíscidos, que se alimentan principalmente de zooplancton; (vi) el descubrimiento de una relación mutualista entre un alga verde epibionta y Daphnia; y (vii) el papel significativo de múltiples factores de estrés sobre la relación algas-bacterias.

PALABRAS CLAVE: *fitoplancton, zooplancton, coleópteros, biodiversidad, estequiometría.*

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INTRODUCTION

Understanding the uniqueness of high-mountain lake food webs requires looking back at their glacial origins. Glacial activity is the primary force behind the formation of most lakes on Earth, especially those at high altitudes and latitudes, regardless of whether they still maintain hydrological connections to glaciers (Wetzel, 2001, Tiberti *et al.*, 2020). The glacial lakes of Sierra Nevada are typically shallower than those in other European mountain ranges, including the Pyrenees. For example, Lake La Caldera, one of the largest in Sierra Nevada, has a maximum depth of only 14 m, which approximates the median maximum depth of Pyrenean lakes (Castillo Jurado, 2003). In contrast, many lakes in the Pyrenees and the Alps exceed 30 m in depth and can reach up to 100 m (Castillo Jurado, 2003, Catalan *et al.*, 2006, Tiberti *et al.*, 2010). This relative shallowness of Sierra Nevada lakes reflects the region's southern location and distinctive glacial history, characterized by smaller glaciers confined to highest elevations near the peaks (Oliva *et al.*, 2014, 2022). Figure 1 illustrates a typical pelagic food web in the Sierra Nevada lakes, showing its connections to the benthic habitat and major trophic compartments. These compartments vary among lakes, depending on geomorphological, hydrological, and trophic characteristics. Generally, these ecosystems are nutrient-poor (ultra-oligotrophic), exhibit low primary production (Straškrabová *et al.*, 1999), and support relatively low species richness (Morales-Baquero *et al.*, 1992, Modenutti *et al.*, 1998). They are dominated by cold stenothermic organisms, making them highly sensitive to climate warming (Vinebrooke & Leavitt, 2005). All high-mountain lakes in Sierra Nevada

are fishless, and it is well established that food web complexity is greatest in such environments (Harper-Smith *et al.*, 2005), where numerous omnivorous consumers feed on diverse prey, while only a few specialize on one or a limited number of prey species (Sánchez-Hernández *et al.*, 2015). Moreover, the near absence of a relevant community of macrophytes may also influence the aquatic food webs in Sierra Nevada. Despite substantial progress, many aspects of food web structure in high-mountain lakes continue to puzzle scientists. For instance, it is unclear why high-mountain lakes often deviate from the typical oligotrophic pattern, where the microbial loop usually dominates over the classical grazing food chain. Further research is also needed to clarify diversity patterns and their trophic roles in food webs. This study reviews historical advances in understanding the aquatic food webs of Sierra Nevada lakes from a trophic perspective, emphasizing their unique features and their contributions to the knowledge of the structure, biodiversity, and functioning of high-mountain lake ecosystems.

The role of these lakes as sentinel ecosystems for tracking global change, further research directions and broader ecological implications on these aspects are included in other paper within this volume of *Limnetica* (Villar-Argaiz *et al.*, 2026).

AQUATIC COMMUNITY STRUCTURE IN SIERRA NEVADA LAKES

Aquatic flora

Limnological studies of the aquatic flora in Sierra Nevada lakes started 50 years ago, with early

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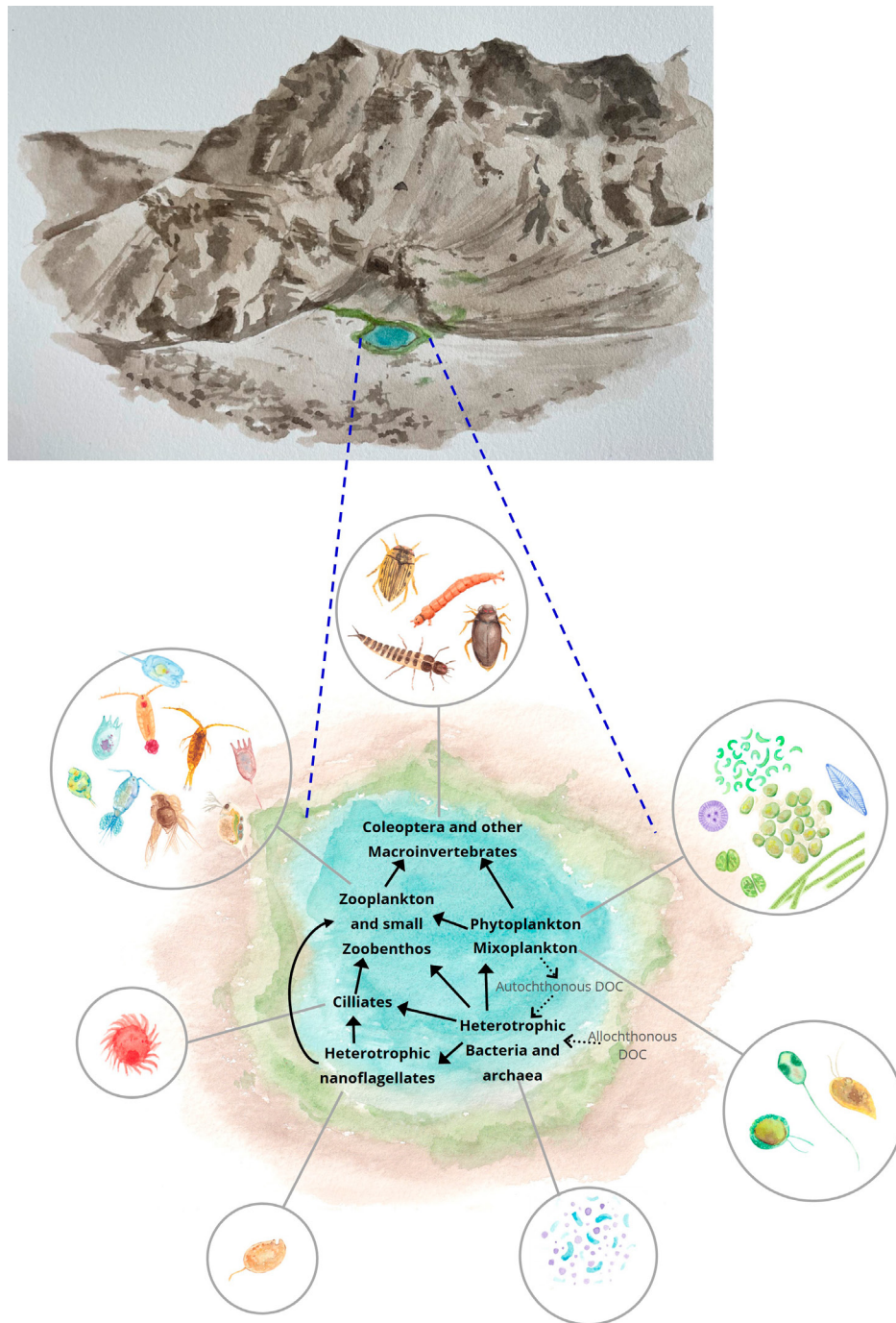


Fig. 1. Artistic illustration of a Sierra Nevada lake and its food web, showing its links to the benthic habitat and the main trophic compartments. Continuous arrows represent matter uptake, and dashed arrows represent dissolved carbon fluxes. (Image credit: C. Otero-Sabio, licensed under CC BY). *Ilustración artística de una laguna de Sierra Nevada y su red trófica, mostrando sus conexiones con el hábitat bentónico y los principales compartimentos tróficos. Las flechas continuas representan el consumo de materia orgánica y las discontinuas los flujos de carbono disuelto. (Crédito de la imagen: C. Otero-Sabio, bajo licencia CC BY).*

studies conducted in Lake La Caldera (Martínez-Silvestre, 1975, Martínez, 1977). Since then, numerous studies have focused on the taxonomy (e.g., Sánchez-Castillo, 1984, 1988) and ecology (e.g., Figueroa *et al.*, 2009) of aquatic flora across numerous Sierra Nevada water bodies.

Sánchez-Castillo (1988), in his study of littoral phytoplankton in 16 Sierra Nevada lakes during the ice-free period, catalogued 149 taxa belonging to several taxonomic classes, including: Cyanophyceae, Dinophyceae, Euglenophyceae, Chrysophyceae, Diatomophyceae, Chlorophyceae and Zygothryx. Subsequent studies have added additional species from these lakes (e.g., Fanes Treviño *et al.*, 2010). Table S1 shows the most up-to-date inventory of phytoplanktonic species recorded in Sierra Nevada lakes, along with epipelagic and epilithic diatoms, as well as certain benthic species occasionally found in the plankton, such as the diatom *Frustulia rhomboides* and the desmid *Euastrum oblongum* (Morales *et al.*, 1992). This compilation includes more than 300 species, while the initial work of Sánchez-Castillo (1988) only recorded 149 species, largely because the earlier study focused on phytoplankton and did not include phytobenthos.

The new species *Chromulina nevadensis* P.M. Sánchez was first recorded by Sánchez-Castillo (1987). This species was described as a mixotrophic Chrysophyceae (Carrillo *et al.*, 1991a) which displays vertical migration, likely driven by light, similar to other flagellates observed in Lake La Caldera (Carrillo *et al.*, 1991b). Additionally, environmental factors such as water turnover rate and nutrient concentrations appear to influence the polymorphism of key species including *C. nevadensis*, *Cyanarcus* sp. and *Ochromonas* sp. (Sánchez-Castillo *et al.*, 2019).

Phytoplankton in Sierra Nevada can be classified into three biological types: non-motile cells (e.g., *Oocystis lacustris* and *Cyanarcus* sp.), flagellated cells (e.g., *Chromulina nevadensis* and *Ochromonas* sp.), and cells of epizoic origin (e.g., *Korshikoviella gracilipes*) (Morales *et al.*, 1992). Some species, such as *Chlorella* sp., exhibit high competitive ability for phosphorus, allowing rapid growth shortly after ice melt, although subsequent nutrient depletion can cause sharp population

declines (Reche *et al.*, 1994). Reche *et al.* (1994) also suggested that infection of phytoplankton by fungi is favored by nutrient limitation. Another notable adaptation is that of the filamentous green alga *Zygnemopsis decussata* to the region's intense ultraviolet (UV) radiation (Figueroa *et al.*, 2009).

Phytobenthos studies in Sierra Nevada have focused on epipelagic and epilithic diatoms (Cameron *et al.*, 1999, Linares-Cuesta *et al.*, 2007, Linares-Cuesta & Sánchez-Castillo, 2007, 2007b, Sánchez-Castillo *et al.*, 2008, Blanco *et al.*, 2019). Linares-Cuesta *et al.* (2007) identified 63 taxa belonging to 29 genera (Table S1, supplementary information, available at <https://www.limnetica.com/en/limnetica>). Small fragilarioid diatoms dominate the epilithon (mainly *Staurosirella pinnata*, *Pseudostaurosira pseudoconstruens*) likely due to their effective colonizing abilities in response to summer water instability (Linares-Cuesta *et al.*, 2007). Epilithic diatoms were studied in Lake La Caldera, where the main species was *Fragilaria rumpens*, a colonising species (Sánchez-Castillo *et al.*, 2008). Five benthic diatom species were described as new taxa to the Iberian Peninsula: *Achnanthydium macrocephalum*, *Caloneis aerophile*, *Encyonema reichardtii*, *Rossethidium nodosum*, and *Surirella bohémica* (Linares-Cuesta & Sánchez-Castillo, 2007b). In Laguna Segunda Lake (belonging to the Siete Lagunas valley), the epilithic species *Fragilaria nevadensis* Linares-Cuesta & Sánchez-Castillo sp. nov. was described as new (Linares-Cuesta & Sánchez-Castillo, 2007a), while, in Lagunillo del Barranco de San Juan, *Encyonema nevadense* S. Blanco & al. sp. nov. was also reported as a new epilithic diatom species (Blanco *et al.*, 2019). *F. nevadensis* has also been recorded in French Alps (Bey & Ector, 2013) and Luxembourg (Coles *et al.*, 2016). Recently, Van de Vijver *et al.* (2021) noted that *F. nevadensis* has been observed in other European locations under different names, and Rivera-Rondón & Catalan (2017) described a closely related conspecific with *Fragilaria* sp. aff. *F. nevadensis*. *F. nevadensis* is conspecific with *F. capucina* var. *acuta* and *F. capucina* var. *acuminata*, and no significant differences were observed among them (Van de Vijver *et al.*, 2021). In contrast, as far as

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we know, *E. nevadense* has not been reported in any other aquatic systems.

Finally, it is worth highlighting the near absence of macrophytes in Sierra Nevada lakes. *Sparganium angustifolium* Michx., an extremely rare macrophyte in high-mountain lakes, has been described and catalogued in Sierra Nevada as an endangered species (Salazar Mendías & Valle Tendero, 2019).

Aquatic fauna in Sierra Nevada lakes

The earliest studies on zooplankton in Sierra Nevada were conducted by Cruz-Pizarro (1978, 1983, 1984). These studies focused primarily on copepods and explored various aspects of zooplankton ecology, including vertical migration (Cruz-Pizarro, 1978), reproduction (Cruz-Pizarro, 1983) and taxonomy (Cruz-Pizarro, 1984). In Lake La Caldera, the diaptomid *Mixodiaptomus laciniatus* showed peak reproductive activity just before freezing the lake, while after the thaw, the population consisted mainly of nauplii and copepodites (Cruz-Pizarro, 1983). Other crustacean species in Sierra Nevada also show similar population dynamics, largely influenced by the distinctive freeze-thaw cycle characteristic of these high-mountain lakes.

In addition to *M. laciniatus*, main copepods inhabiting Sierra Nevada include *Diaptomus cyaneus*, *Acanthocyclops vernalis*, *Paracyclops fimbriatus* and *Eucyclops serrulatus* (Hernández-Márquez, 1986, Morales-Baquero et al., 1992, Table S2, supplementary information, available at <https://www.limnetica.com/en/limnetica>). Regarding zooplankton groups, 12 copepod species, 10 cladoceran species and 29 rotifer species have been recorded in Sierra Nevada (Table S2). Nevertheless, these numbers should be considered with caution because most of the Sierra Nevada lakes were only sampled in their littoral zone, and many of these surveys were conducted roughly 40 years ago, highlighting the need for updated research (see Villar-Argaiz et al., 2026).

Most zooplankton species identified are benthic or littoral, being only a few truly planktonic forms: the copepods *M. laciniatus* and *D. cyaneus*; the cladocerans *Daphnia pulex*,

Daphnia pulicaria and *Bosmina longirostris*; and the rotifers *Hexarthra bulgarica*, *Notholca squamula*, and *Polyarthra dolichoptera* (Morales-Baquero et al., 1987a, Morales-Baquero et al., 1992, Conde-Porcuna et al., 2021). In general, the composition of species is recurrent among lakes (Morales-Baquero et al., 1992). For instance, the rotifers *Euchlanis dilatata* and *Trichocerca relicta* are present in about 80% of Sierra Nevada lakes (Morales-Baquero, 1987b).

Rotifers from the littoral zone in Sierra Nevada lakes were extensively studied by Morales-Baquero (1987b), who described a new subspecies (*Lepadella quinquecostata nevadensis* subsp. nov.), and reported three species for the first time in Spain: *Trichocerca (Diurella) relicta*, *Cephalodella gibba microdactyla* and *Lecane (Heminostyla) kluchor*.

Among environmental variables, temperature in Sierra Nevada seems to be one of the main factors controlling zooplankton communities, by probably affecting sex-ratios and body size in copepods (Cruz-Pizarro, 1983, 1984), as well as in rotifers (Morales-Baquero, 1988) and cladocerans (Ramos-Rodríguez et al., 2022). Mineralization is another important determinant, with low-conductivity lakes typically supporting high densities of planktonic rotifers (Morales-Baquero et al., 1989). Hydrological characteristics also play a role. Morales et al. (2019) demonstrated that zooplankton abundance during the ice-free period was approximately twice as high in closed lakes (without permanent outflows) compared to open lakes (with outlets), highlighting the impact of advective losses due to water flow. Additionally, UV radiation could trigger rotifer egg production (Cruz-Pizarro et al., 1998) and affect zooplankton growth rates, although such effects are likely species-specific (Villar-Argaiz et al., 2012).

Daphnia species

The genus *Daphnia* is traditionally considered a keystone group in the trophic chain of many aquatic systems (e.g., Seda & Petrussek, 2011). In Sierra Nevada, *Daphnia* is also one of the most relevant ecological genera within lake food webs. Beyond its ecological importance, *Daphnia* is an easy-to-culture model organism widely used in

research due to several advantageous traits: (i) its convenient size for experimental work (e.g., De Meester *et al.*, 2023); (ii) its high sensitivity to environmental perturbations (e.g., Atshuler *et al.*, 2011); (iii) its distinct phototactic behaviour (e.g., Cousyn *et al.*, 2001); (iv) its capacity for both sexual and asexual reproduction, which enables researchers to distinguish genetic from non-genetic effects (e.g., Ebert, 2022); and (v) its ability to produce diapausing forms, a key adaptation for dispersal across time and space (e.g., Slusarczyk *et al.*, 2019).

Because of all these traits, *Daphnia* is regarded as a model organism across multiple research fields, including reproductive biology, resurrection ecology, climate change ecology, genetic diversity, dispersal dynamics, and host-epibiont interactions. In Sierra Nevada, *Daphnia* has likewise served as a model organism for exploring these biological processes.

Genetic analyses by Conde-Porcuna *et al.* (2021) demonstrated that *Daphnia cf. pulicaria* (sensu Alonso, 1996) is the sole daphnid species inhabiting Sierra Nevada lakes where this genus is present except for Borreguil Lake, which is instead inhabited by *D. cf. pulex* (sensu Hebert, 1995). Prior to this study, earlier research in Sierra Nevada had misidentified *Daphnia pulicaria* as *Daphnia pulex* (e.g., Morales-Baquero *et al.*, 1992), largely because species delimitation within the *Daphnia pulex-pulicaria* complex is extremely difficult due to their negligible morphological differentiation (e.g., Marková *et al.*, 2007, Burillo *et al.*, 2019).

Conde-Porcuna *et al.* (2021) documented the first occurrence of *D. cf. pulex* in a European high-mountain lake. These individuals are closely related to those described by Mergeay *et al.* (2006) in Africa, identified as an invasive hybrid between *D. cf. pulex* and *D. pulicaria*. It colonized Borreguil Lake in Sierra Nevada ~70 years ago and has maintained a stable genetic structure since its arrival. Similarly, *D. cf. pulicaria*, the only lineage present in other Sierra Nevada lakes, also showed no temporal genetic variation (Conde-Porcuna *et al.*, 2021). Henceforth, we refer to *D. cf. pulicaria* and *D. cf. pulex* as *D. pulicaria* and *D. pulex*, respectively.

Conde-Porcuna *et al.* (2021) also detected

genetic differences in *Daphnia* among several Sierra Nevada lakes, suggesting that water mineralization (conductivity and calcium concentration) and total nitrogen concentration could be associated with this variation. Lake Borreguil, the only lake inhabited by *D. pulex*, is characterized by low concentrations of both calcium and nitrogen. Building on this, Ramos-Rodríguez *et al.* (2022) conducted a life history experiment with *D. pulex* and found a positive synergistic effect of calcium and temperature on reproductive success under high food conditions. While an increase in temperature to 21° C greatly reduced survival, populations were still able to thrive at low calcium concentrations (<0.25 mg Ca L⁻¹) when food availability was high (2 mg C L⁻¹). Under climate change scenarios with high food resources, *Daphnia* populations may exhibit enhanced tolerance to low calcium concentrations, potentially supporting higher population growth rates (Ramos-Rodríguez *et al.*, 2022). Further research is necessary to compare the population responses of *D. pulicaria* and *D. pulex* to environmental factors in Sierra Nevada lakes.

Life cycle of Daphnia

In Sierra Nevada, research on *Daphnia* has been conducted primarily in Río Seco Lake through both field and laboratory studies, although additional studies have also been performed in Lake La Caldera and Borreguil lake, among others.

Pérez-Martínez *et al.* (2007) described a key reproductive trade-off in *Daphnia*, in which individuals allocate resources either to production of active offspring (via subitaneous eggs) or to future survival through the formation of diapausing forms (ephippia). Moreover, this genus exhibits a range of reproductive strategies, including cyclical parthenogenesis with sexual reproduction and obligate parthenogenesis, where reproduction occurs exclusively asexually (Hebert *et al.*, 1988, Innes *et al.*, 2000).

Each spring in Sierra Nevada, *Daphnia* are expected to recolonize the lakes after the thaw by hatching from ephippia, as observed in Río Seco Lake (Pérez-Martínez *et al.*, 2007, 2013, Conde-Porcuna *et al.*, 2009). In this lake, no large

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or egg-bearing individuals were detected at the beginning of the ice-free period over six consecutive years, suggesting that each year's population originates exclusively from ephippial hatching.

In a field experiment in Río Seco Lake using sediment emergence traps, Pérez-Martínez et al. (2013) found that the hatching period was restricted to a three-week window following ice thaw. Their results indicated that light exposure at ice break-up induced dormancy termination in *D. pulicaria*. Complementary laboratory experiments revealed no hatchlings under dark conditions, while hatching rates were unaffected by either photoperiod or temperature; although the time of hatching was affected by temperature.

Previous studies have claimed that changes in photoperiod and temperature can trigger dormancy termination in zooplankton (Brendonck & De Meester, 2003, Gyllström & Hansson, 2004, Vandekerckhove et al., 2005, Dupuis & Hann, 2009). However, Pérez-Martínez et al. (2013) reported that in high-mountain lakes, such as those in Sierra Nevada, light availability is the primary factor initiating hatching. Supporting this, Ślusarczyk & Flis (2019), studying *D. magna* from an urban pond in Warsaw (Poland), confirmed that light duration and intensity play a central role in dormancy termination and hatching rates. These findings suggest that the role of photoperiod and temperature may depend on the lake characteristics. In permanent systems, photoperiod and temperature may trigger dormancy termination, whereas in temporary waters, other factors appear to be more critical cues for hatching.

High-mountain lakes have been considered “temporary” systems for zooplankton due to their short growing seasons and low winter survivorship of active individuals (Pérez-Martínez et al., 2013). In Sierra Nevada, the lakes remain frozen around eight months. While water refilling events trigger hatching in temporary waters that dry up during summer, in “temporary” lakes that freeze for extended periods, light availability and intensity, rather than photoperiod, appear to be the main triggers (Pérez-Martínez et al., 2013, Ślusarczyk & Flis, 2019). In another Spanish lake (Lake Cimera), underwater photosynthetically active radiation (PAR) during the ice cover often falls

below $5 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Granados et al., 2020), and Ślusarczyk & Flis (2019) reported a marked decline in the hatching of *Daphnia* ephippia at $3.5 \mu\text{mol m}^{-2} \text{s}^{-1}$, with scarce hatchlings.

Once *Daphnia* individuals hatched from ephippia, they re-colonize Sierra Nevada lakes, although reproduction via subitaneous eggs seems to be low (Pérez-Martínez et al., 2007). In fact, *Daphnia* individuals need to rapidly invest in dormant eggs to guarantee long-term persistence in high-mountain lakes with a short growing season and harsh climatic conditions (Decaestecker et al., 2009, Barea-Arco et al., 2001, Pérez-Martínez et al., 2007, 2013, Conde-Porcuna et al., 2011, 2014).

This rapid investment in dormant eggs is facilitated in obligate parthenogenetic species, which avoid the costs associated with producing males, as fertilization is unnecessary (Innes et al., 2000, Decaestecker et al., 2009). Supporting this, Pérez-Martínez et al., (2007) hypothesized that *D. pulicaria* in Río Seco Lake is an obligate parthenogenetic population, based on the observation of only a single male over three years of study. This hypothesis was later confirmed by Conde-Porcuna et al. (2021), who reported a low genotype richness and high deviations from Hardy–Weinberg equilibrium (excess of heterozygotes) across all *Daphnia* haplotypes in Sierra Nevada, including *D. pulicaria* and *D. pulex*. They also observed highly significant negative inbreeding coefficients (F_{IS}), indicating that repeated genotypes result from clonal reproduction. In consequence, all *Daphnia* populations in Sierra Nevada reproduce via obligate parthenogenesis.

Obligate parthenogenetic *Daphnia* initially produce ephippial eggs after a short period producing subitaneous eggs. The number of subitaneous eggs serves as a good predictor of food availability in field studies (e.g., Mooij et al., 2003), and ephippial reproductive rates have been calculated by ephippial counts alone (e.g., Koch et al., 2009). However, subitaneous eggs may be aborted (Threlkeld, 1979), and Conde-Porcuna et al. (2011) were the first to document ephippial egg abortion in *Daphnia* through both laboratory and field observations. They reported a low number of healthy ephippial eggs per ephippium, a high

number of empty ephippia, as well as elevated rates of subitaneous egg abortion. Laboratory experiments conducted under dynamic conditions—where photoperiod and temperature were adjusted to reflect field fluctuations—closely matched field observations, highlighting the relevance of simulating natural environmental variability to accurately capture field reproductive dynamics. These findings suggest that estimates of ephippial reproduction may have been overestimated when based only on ephippia counts without considering the number of viable eggs per ephippium.

Later, Conde-Porcuna *et al.* (2014), investigated *in situ* production of ephippia and ephippial eggs in Río Seco Lake and found that higher food availability can enhance ephippial reproduction and increase the number of healthy ephippial eggs. They proposed that, after the onset of ephippia production, well-nourished *Daphnia* are more likely to produce viable ephippial eggs. In this case, food sources include the epibiont alga *Korshikoviella gracilipes*, which grows on *Daphnia*—a host-epibiont interaction discussed further below.

Zooplankton stoichiometry

Examining the elemental composition of organisms through a stoichiometric lens—specifically their carbon, nitrogen, and phosphorus (C:N:P) ratios—has provided valuable insights into species success, nutrient recycling, and energy flow in ecosystems, thereby improving our understanding of food web structure in lakes and other aquatic ecosystems (Sterner & Elser, 2002). This area of research, known as Ecological Stoichiometry (ES), has significantly advanced our understanding of ecological phenomena, including:

Homeostasis

A key discovery in ES is that autotrophs exhibit flexible elemental composition in response to nutrient availability, whereas consumers maintain a more rigid balance due to the need to maintain homeostasis in their internal environment (Sterner & Elser, 2002). However, early research in Lake La Caldera revealed that substantial variation in phytoplankton stoichiometry—driven

by factors such as temperature and phosphorus availability—resulted in unexpected variability zooplankton elemental composition. These observations challenged the classical ES assumption of strict consumer homeostasis (Villar-Argaiz *et al.*, 2002a). Through the first full ontogenetic study of a copepod species, we identified flexible homeostasis, supporting the concept of rheostasis, in which organisms actively adjust their internal composition in response to environmental changes (Villar-Argaiz *et al.*, 2002a).

Life history strategies

Research in Sierra Nevada has been pioneering in linking organismal stoichiometry to life-history strategies (Villar-Argaiz *et al.*, 2002a). Variations in copepod carbon-to-phosphorus (C:P) ratios throughout their life cycle were closely tied to changes in both C and P content. Copepods rapidly accumulated C during their high-growth larval and juvenile stages, which corresponded with a reduction in the neutral-to-polar lipid ratio. In adulthood, C accumulation slowed, maintaining a high neutral-to-polar lipid ratio to support survival and reproduction. Meanwhile, P content was highest in larvae and declined with age, showing a strong correlation with growth rate. These findings were highly influential in the field of stoichiometry, contributing—along with studies on other terrestrial and aquatic organisms—to the formulation of the Growth Rate Hypothesis (Elser *et al.*, 2003). To further investigate the mechanisms behind P content, we conducted the first study examining intra-stage variation in phosphorus levels (Carrillo *et al.*, 2001). We found that peak P content occurred during the most mitotically active phase of each developmental stage, just prior to molting during ecdysis.

Given the essential role of P for life, it is unsurprising that organisms have evolved strategies to survive in environments typically limited in this nutrient. One such strategy, the Phosphorus Allocation Hypothesis, proposes that cladocerans have smaller genomes than copepods due to preferential P allocation toward RNA production to support rapid growth (Hessen *et al.*, 2010). By analyzing over 400 zooplankton individuals, we

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confirmed this hypothesis: cladocerans exhibited a higher RNA content relative to DNA, with an average RNA:DNA ratio eight times greater than that of copepods (Bullejos et al., 2014a). Subsequent research extended this framework to insects. The hypothesis, later redefined as the Growth Rate–Genome Size–Nutrient Limitation Hypothesis, revealed that differences in RNA versus DNA allocation represent an evolutionary trade-off between biological strategies: holometabolous insects prioritize higher growth rates (and thus RNA content) at the expense of having smaller genomes (Villar-Argaiz et al., 2021). Together, these studies advance ecological theory by showing how P availability shapes growth, reproduction, and evolutionary strategies, fundamentally influencing an organism's niche, life history strategy, and ecological success.

Consumer-resource dynamics

A key challenge in systems ecology is understanding energy flow within trophic networks, where stoichiometry plays a crucial role, especially at the plant-herbivore interface. Herbivores, with high phosphorus (P) and nitrogen (N) demands, often consume food that is relatively deficient in these elements relative to carbon (C). Furthermore, the marked variations in P content throughout the ontogenetic development of individual zooplankton species (Villar-Argaiz et al., 2002a) indicate that nutrient limitation can arise not only between species but also within species across different life stages. To investigate this, zooplankton growth was analyzed using %RNA as a proxy across a range of phytoplankton food qualities, revealing a unimodal growth pattern best described by a second-degree polynomial relationship (Bullejos et al., 2014b). The solution to the first derivative of this equation provided crucial insights into the nutrient limitation threshold, known as the Threshold Elemental Ratio—the point at which growth limitation shifts from C to P. The kurtosis of the growth curve reflected sensitivity to food quality, linking directly to the Elemental Niche concept proposed by Peñuelas (2019). The findings showed that nutrient limitation thresholds vary across ontogeny, with juvenile stages being particularly susceptible to

P-limitation. Parallel research has demonstrated that unimodal responses to environmental factors are widespread among other planktonic taxa, adding complexity to ecological interactions and affecting organismal adaptation (Medina-Sánchez et al., 2013). These findings underscore the importance of considering both stoichiometric constraints and ontogenetic variability when predicting consumer–resource dynamics in aquatic ecosystems.

Integration of ecological theories

To bridge stoichiometric and metabolic perspectives, we conducted research across 22 high-mountain lakes in the Pyrenees and Sierra Nevada (Bullejos et al., 2014a). According to Brown's Metabolic Theory of Ecology (MTE), higher temperatures are expected to increase organismal growth rates (Brown et al., 2004) and, consequently, RNA demand, as predicted by stoichiometric principles. Our results confirmed a positive correlation between RNA content and temperature under nutrient sufficient conditions. However, in P-deficient ecosystems, this relationship was reversed, aligning with stoichiometric expectations (Bullejos et al., 2014a). These findings demonstrate that temperature impacts on organisms depend on complex interactions involving growth, RNA allocation, and nutrient availability, highlighting key mechanisms that unify MTE and ES.

Aquatic coleopterans (macroinvertebrates)

Coleopterans are a fundamental component of Sierra Nevada high-mountain lakes, both in terms of biomass and diversity. Water beetle assemblages from these lakes consist of 22 species (Table S3, supplementary information, available at <https://www.limnetica.com/en/limnetica>), belonging to 2 suborders and 6 families (Millán et al., 2014, Abellán et al., 2022). Although this richness can be considered low in comparison with, for example, headwater streams, it harbours highly specialized taxa including three species endemic to the Sierra Nevada massif—*Agabus nevadensis*, *Hydroporus sabaudus sierranevadensis* and *Hydroporus*

normandi alhambrae—and three endemic species to the Iberian Peninsula—*Hydroporus nevadensis*, *Helophorus nevadensis* and *Ochthebius semotus* (Millán *et al.*, 2013, 2014). The most abundant aquatic coleopterans in these high-mountain lakes are, by far, the diving beetles from the Dytiscidae family, with *Agabus nevadensis*, *Hydroporus marginatus*, *Hydroporus sabaudus sierranevadensis* and *Boreonectes ibericus* being highly prevalent across most lakes (Abellán *et al.*, 2013). Other commonly occurring species include *Helophorus glacialis* (Helophoridae), *Limnebius truncatellus* (Hydraenidae) and *Enochrus fuscipennis* (Hydrophilidae). In contrast, the remaining species occur irregularly or only occasionally, such as reophilic Elmidae, which likely drift into these lentic ecosystems from stream inlets (Abellán *et al.*, 2013). Similarly, most other macroinvertebrate in these lakes show irregular occurrences, primarily in low-altitude lakes, and are generally present at low abundances. Only a few taxa belonging to the families or subfamilies Planariidae (Platyhelminthes), Sphaeriidae (*Euglesa* sp.; Mollusca), Lumbriculidae (Annelida), Tanypodinae, Chironominae and Orthocladinae (Diptera) are regularly recorded in most lakes (Ortego *et al.*, 2025).

Dytiscids play a crucial role in the food web of these lakes that lack fish or host waterbirds only occasionally. Indeed, in the highest elevation lakes where amphibians and Odonata do not breed, dytiscids are the only top predators together with the water boatman *Sigara nigrolineata*, whose flying adults can be detected at the end of the snow-free season, likely coming from lowland ponds (own observations). As generalist predators, both adult and larval dytiscids feed on zooplankton, other aquatic invertebrates, larval amphibians, and fish (Culler *et al.*, 2014). Recent studies in Sierra Nevada high-mountain lakes have shown that Dytiscidae species occupy broad trophic niches, primarily feeding on zooplankton and other invertebrates, with intraguild predation and likely cannibalism, playing significant roles (Carbonell *et al.*, 2025). Interestingly, *Helophorus glacialis*—typically classified as a herbivore or, at most, an omnivore (Millán *et al.*, 2014)—has also been observed acting as a top predator in

Aguas Verdes Lake and as a secondary predator in Cuadrada Lake (Millán *et al.*, 2014).

Unlike adult dytiscids, which are often inefficient at hunting active preys and often scavenge on decaying animal matter, the larvae are exclusively predaceous (Larson *et al.*, 2000) and employ a variety of hunting strategies, including active chase and sit-and-wait tactics to capture prey (Yee, 2010; Culler *et al.*, 2014). They can also select certain types of prey over others: for example, larval *Agabus* show a preference for Diptera larvae, whereas some Hydroporinae larvae, such as *Hydroporus* and *Boreonectes*, have elongated nasales likely adapted for capturing microcrustaceans (Culler *et al.*, 2014).

Intraguild predation (IGP) is common among dytiscids, with large-bodied species acting as top predators in fishless ponds consuming smaller dytiscids (Culler *et al.*, 2014). Cannibalism is also widespread among larvae and serves as a density-dependent mechanism regulating population dynamics, while it is less common in adults due to gape-size limitations, so it likely plays an underappreciated role in structuring dytiscid populations. This is in line with recent results from Sierra Nevada lakes, where *Agabus nevadensis* have been shown to feed on conspecifics occupying the same trophic level (Carbonell *et al.*, 2025). Beyond direct predation, dytiscid presence exerts significant non-consumptive effects on prey, such as behavioral, physiological and life-history modifications that can influence prey fitness (Culler *et al.*, 2014). For instance, the presence of dytiscid predators can affect daphnid migration strategies and body size (Herwig & Schindler, 1996), or alter ovoposition, larval activity and body size in mosquitoes (Ohba *et al.*, 2012). These findings suggest that dytiscid-induced fear responses have consequences on the whole ecosystem, potentially outweighing direct predation effects.

Predation dynamics in aquatic systems are influenced by both biotic and abiotic factors. For instance, habitat complexity affects dytiscid foraging strategies, shifting their behavior from active hunting to sit-and-wait predation (Yee, 2010). This might explain why lakes with higher habitat diversity, such as Aguas Verdes, support a more complex food web with multiple trophic levels, while lakes with lower habitat diversity,

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such as Lake La Caldera, exhibit fewer trophic levels but a more complex trophic structure, with dytiscids exploiting a wide range of food sources (Carbonell et al., 2025). Temperature is another critical driver affecting metabolic rates and foraging efficiency. Higher temperatures shorten the dive duration and increase dytiscid surfing frequency, therefore reducing available foraging time (Calosi et al., 2007, Culler et al., 2014). Given ongoing climate change, understanding temperature-mediated shifts in dytiscid predation is of particular interest in these lakes, where they function as top predators.

Sierra Nevada lakes provide an exceptional natural laboratory for filling knowledge gaps regarding the role of dytiscids in structuring lentic freshwater food webs. Future research should investigate the prevalence of generalist versus specialist feeding strategies across dytiscid species and life stages, the importance of intraguild predation and cannibalism, as well as the extent and consequences of non-consumptive predator effects. Finally, as global environmental changes—such as habitat degradation and climate shifts continue to alter aquatic ecosystems, it is crucial to explore how these factors reshape dytiscid predation dynamics and their cascading effects on community structure and ecosystem functioning. Climate-induced shifts may also facilitate the arrival of aquatic beetle species from lower elevations, potentially leading to novel biotic interactions that could jeopardize the survival of the exclusive communities in Sierra Nevada lakes.

Biodiversity of aquatic organisms in Sierra Nevada lakes

Several studies in Sierra Nevada lakes have investigated ecological diversity and species richness, most commonly using the Shannon-Wiener index. In general, both planktonic species richness and phytoplankton Shannon-Wiener diversity are generally low, primarily due to the homogeneous abiotic environments of these lakes, which are typically small, shallow, and dominated by littoral zones (Morales-Baquero et al., 1992, Pérez-Martínez et al., 2020). For these reasons, zooplankton communities are dominated by littoral and benthic organisms, with relatively

few planktonic species. Nevertheless, low-conductivity lakes can support high densities of typically planktonic rotifers (Morales-Baquero et al., 1989). Regarding coleopterans, due to their high feeding rates and their role as top predators, dytiscids can reduce macroinvertebrate and zooplankton abundance and biomass. This predatory pressure may trigger trophic cascades, potentially lowering overall diversity. Moreover, the prevalence of IGP in dytiscids likely influences species coexistence and the overall diversity of their communities (Culler et al., 2014).

Phytoplankton communities are characterized by Shannon-Wiener diversity values of 2–4 bits per individual, although temporal patterns vary among lakes (Sánchez-Castillo et al., 1989). Functional diversity of phytoplankton is also relatively low, as reported for Aguas Verdes Lake (Grossman et al., 2016). Nevertheless, *in situ* experiments in another Sierra Nevada lake showed that UV radiation increased the phytoplankton Shannon-Wiener diversity, an effect that was reversed by the addition of P (Delgado et al., 2009). For other aquatic flora, Sánchez-Castillo et al. (2008) reported that the diversity of epilithic diatoms typically exceeds 1.0, with lower values occurring when *Fragilaria rumpens* dominates. Diversity was observed to show higher values immediately after ice melt, probably due to the survival of resistant diatom forms over the winter. Desmids also represent a relevant group of benthic algae in these lakes, thriving under the low mineralization and slightly acidic conditions of these waters (Sánchez-Castillo et al., 2019). In this context, Coesel et al. (2001) developed the "nature conservation value" (ncv) index, which incorporates biodiversity and population metrics based on desmid communities. Several Sierra Nevada lakes exhibit high ncv scores, making the index a useful tool for evaluating the conservation status of these systems (Sánchez-Castillo et al., 2019).

Finally, one of the most remarkable findings regarding diversity in Sierra Nevada lakes was reported by Reche et al. (2005). Their study confirmed the species–area relationship proposed by island biogeography theory (MacArthur & Wilson, 1967), demonstrating that bacterial diversity increases with lake area. Reche et al. (2005) also

suggested high dispersion rates of these organisms across Sierra Nevada lakes. Although bacterial diversity was unrelated to lake isolation, the study was notable for confirming macroecological patterns using microorganisms, often overlooked in ecological theory. More recently, the development and application of DNA-based molecular techniques (quantification and sequencing) has greatly advanced our understanding of microbial biodiversity and functioning in these lakes. These methods have revealed critical roles for bacterial and archaeal communities in key ecological processes such as denitrification in lake sediments (Castellano-Hinojosa *et al.*, 2017), the efficiency of reactive nitrogen removal in lake and river sediments (Castellano-Hinojosa *et al.*, 2023), and the biotic changes due to intense Saharan dust deposition on lake sediments (Castellano-Hinojosa *et al.*, 2024).

TROPHIC INTERACTIONS WITHIN THE AQUATIC COMMUNITY

Phytoplankton-bacterioplankton interactions

The microbial communities of Sierra Nevada high-mountain lakes typically exhibits a greater proportion of autotrophic biomass and activity relative to heterotrophic processes, unlike most oligotrophic ecosystems worldwide (Medina-Sánchez *et al.*, 1999, 2002, 2022, Carrillo *et al.*, 2006). This peculiar biotic structure, which diverges from patterns commonly observed in other oligotrophic ecosystems (Biddanda *et al.*, 2001, Cotner & Biddanda, 2002), is largely explained by the specific composition of the phytoplankton community and its interaction with bacterioplankton.

Numerous observational and experimental studies in these lakes have consistently shown that algae and bacteria establish a “basal” commensalistic relationship (Table 1), which is sustained by (i) the ability of algae to release newly photosynthesized organic carbon, whether photosynthesis is tightly coupled to growth (Lignell, 1990) or not (Berman-Frank & Dubinsky, 1999); (ii) the bacterial reliance on this algal excretion of organic carbon (EOC) –composed of simple organic molecules readily consumed by bacteria–

over other organic carbon sources such as ‘old’ autochthonous or scarce allochthonous carbon from the small, unvegetated catchments (Medina-Sánchez *et al.*, 2002, 2010); and (iii) the adaptation of bacterioplankton to high UVR levels through effective (photo)repair mechanisms, that allows bacteria to grow effectively leveraging the higher EOC rates under UVR (Carrillo *et al.*, 2002, 2008a, Medina-Sánchez *et al.*, 2002, Durán *et al.*, 2016). However, this algae-bacteria relationship can temporarily shift from commensalism to competition for mineral nutrients, depending largely on the algal N:P ratio and P availability (Villar-Argaiz *et al.*, 2002b, Table 1).

Although strictly autotrophic, non-flagellated algae (e.g., *Dictyosphaerium*, *Monoraphidium*, *Cyclotella*...) are commonly present and can dominate mid-summer phytoplankton, mixotrophic algae (e.g., *Chromulina*, *Ochromonas*, *Rhodomonas*, *Amphidinium*) are a key component of the algal community during most of the ice-free period (Medina-Sánchez *et al.*, 1999, 2004, Delgado-Molina *et al.*, 2009). These mixotrophs, which combine both photosynthesis and phagotrophy within a single cell as a nutritional strategy, account for the divergence of these lakes from the typical microbial pattern observed in oligotrophic systems. Functioning as photoheterotrophs, mixotrophic algae (mixoplankton, Fig. 1) use sunlight to generate energy (ATP) and reducing power (NADPH) without directly incorporating carbon, while simultaneously acquiring carbon and essential nutrients (N, P) by phagotrophic consumption of bacteria (Wilken *et al.*, 2014, Cabrerizo *et al.*, 2019a). This dual strategy is particularly advantageous under the nutrient-poor conditions of these lakes, allowing mixotrophs to exert a dual control on bacterioplankton: they effectively “farm” bacteria by providing them with “cheap” organic carbon, and at the same time harvest the expensive nutrient-rich bacteria to meet their own needs. This dual control is so remarkable that it becomes a predictive variable for (specific) bacterial production (Medina-Sánchez *et al.*, 2004), and it has been artistically described as a “neither with nor without you” relationship, to emphasize their mutual dependence, i.e., bacteria rely on algae for carbon, and algae

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Table 1. Set of experiments conducted in high-mountain lakes of Sierra-Nevada to study how interaction among multiple global-change drivers impacts algae-bacteria relationships. Only experiments showing results on this relationship or on mixotrophs are included. *Experimentos realizados en las lagunas de alta montaña de Sierra Nevada para analizar cómo las interacciones entre múltiples causantes del cambio global afectan a la relación algas-bacterias. Solo se incluyen los experimentos que presenten resultados sobre esta relación o sobre organismos mixótrofos.* Containers: microcosms (0.1 to 100 L), mesocosms (>100 to 3000 L). Time: short-term (hours to 1 day), mid-term (1 week to < 1 month), long-term (\geq 1 month). Radiation: PAR (photosynthetically active radiation), UVB (ultraviolet radiation B, 280-320 nm wavelength), UVA (ultraviolet radiation A, 320-400 nm wavelength), UVR (ultraviolet radiation A+B). Nutrients: C (carbon), N (nitrogen), P (phosphorus). Biota: HMFW (heterotrophic microbial food web), HNF (heterotrophic nanoflagellates).

Manipulating factors	In situ experimental approach	Temporal scale	Main results	References
Zooplankton concentration	microcosms	mid-term	Algae-bacteria commensalism is enhanced via increased animal P-excretion	Reche et al., 1997
Nutrient (P) addition at fixed N:P ratios	microcosms	short-term	Algae-bacteria competition for P is enhanced via increased organic C excretion by P-enriched algae	Villar-Argaiz et al., 2002b
Nutrient (P) addition at fixed N:P ratios	microcosms	mid-term, at 3 points of ice-free period	Acute proliferation of ciliates with P-enriched bacteria and NP-balanced algae. Strong algal growth initially dominated by strict autotrophs; moderate or no algal growth initially dominated by mixotrophs showing their metabolic plasticity (growth vs. P-storage strategies)	Carrillo et al., 2008b
Natural UVR quality x depth	microcosms	short-term	Algal photosynthesis inhibited by UVA and UVB, bacterial growth inhibited by UVB but enhanced by UVA and PAR; algae-bacterial commensalism enhanced by full solar radiation	Carrillo et al., 2002
Natural UVR quality x increased stratification	microcosms	short-term	Algae-bacteria commensalism is strengthened by full UVR and increased stratification; the opposite is found in UVR-opaque lake out of Sierra Nevada (Conceja, Lagunas de Ruidera)	Carrillo et al., 2015
Natural UVR quality x nutrient (P) addition at fixed N:P ratios	microcosms	short-term	Algae-bacterial mutualism is reinforced under UVR and P enrichment with P-deficient algae, and persists with P-sufficient algae	Medina-Sánchez et al., 2006
Natural UVR quality x nutrient (P) addition at fixed N:P ratios x removal of algae	microcosms	short-term	Bacterial response to spectral solar radiation depends on fresh-C released from algae (commensalism), and it is modulated by P-availability and bacterial N:P composition	Medina-Sánchez et al., 2002

Cont.

Cont.

Manipulating factors	<i>In situ</i> experimental approach	Temporal scale	Main results	References
Natural UVR x nutrient (P) addition in gradient	mesocosms	long-term	HMWF (without HNF) transiently and unimodally responds to P-enrichment gradient with moderate positive effect of UVR at intermediate P-levels, during P-availability phase. Strong bloom of a strict autotrophic species and collapse of HMFw and mixotrophs during P-depleted period P-pulse reverses positive effect of UVR on algal diversity and evenness at long-term; strong loss of algal biodiversity during P-depleted period	Medina-Sánchez et al., 2013 Delgado-Molina et al., 2009
Natural UVR x nutrient (N,P) addition	coupled with <i>in situ</i> mesocosms (split-plot design)	long-term and mid-term	Strict autotrophic algae linearly respond to P-enrichment gradient, and a moderate negative UVR-effect which is intensified with the P-gradient	Carrillo et al., 2008a
Natural UVR x nutrient (N,P) addition frequency (press vs. pulse)	mesocosms	long-term	UVR x Nutrient synergistically favors strict autotrophic against mixotrophic algae, experimentally anticipating and supporting the decline in mixotrophs observed at long term	Carrillo et al., 2017
Natural UVR x nutrient (N, P) addition x increased temperature	mesocosms	long-term	A high frequency of low nutrient inputs (press) under UVR favored mixotrophs and their dual control on bacteria; a unique nutrient input of the same final magnitude (pulse) favored the strict autotrophs	Cabrerizo et al., 2017
Natural UVR x nutrient (P) addition x temperature abrupt shift	mesocosms (split-plot design)	short-term	The effect of the three-factors interaction on algae-bacteria commensalism depends on the lake. In a colder lake, algae-bacteria uncoupled while in a warmer lake the coupling is accentuated	Durán et al., 2016
Nutrient (P) addition x organic carbon (C) addition	mesocosms	mid-term	Algae-bacteria mutualism is weakened under all experimental conditions	Durán et al., 2020
Natural UVR x nutrient (P) addition x organic carbon (C) addition	mesocosms	mid-term	Bacterioplankton is synergistically co-limited by C and P, and the type of CP-colimitation is shaped by algal predation	Dorado-García et al., 2014
Saharan dust addition in gradient x increased constant or fluctuating temperature	mesocosms coupled with <i>ex situ</i> microcosms	Long-term; mid-term at 3 points of the long-term experiment	Based on ecoenzyme activities, while C-addition does not affect microbial metabolism, P-addition promotes algal growth, leading bacteria to be more limited by nutrients (mainly P and secondarily by N) than by energy (C), with UVR playing a minor role Under the most complex scenario (UVR x P x C), high resistance of ecosystem metabolic balance due to high resistance of mixotrophs and algae-bacteria commensalism. High resilience of strict phototrophs and the algae-bacteria commensalism While dust addition alone strengthens algae-bacteria coupling (via commensalism), an inflection occurred with high temperature at intermediate dust loads, leading to algae-bacteria decoupling in the long term	Velasco-Ayuso et al., 2017 Cabrerizo et al., 2019b Vila-Duplá et al., 2024

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depend on bacteria for nutrients. The discovery of this mutualistic interaction represents a shift from the traditional paradigm of aquatic food webs in high-mountain lakes (Medina-Sánchez et al., 2004). Traditionally, algae release organic carbon that fuels bacterial growth, as bacteria are more efficient at absorbing dissolved nutrients at low concentrations; microzooplankton then consume bacteria, releasing some immobilized nutrients back to the water for algae to use. In contrast, the new paradigm, shows that mixotrophic algae directly utilize bacteria as a source of nutrients (and carbon) to sustain their own growth (Medina-Sánchez et al., 2004, Mitra et al., 2014). This mixed feeding mode provides several adaptive advantages over other planktonic organisms in high-mountain lakes: (i) more efficient nutrient acquisition than strictly autotrophic algae under oligotrophic conditions; (ii) the ability to thrive at lower prey densities than heterotrophic nanoflagellates and ciliates; and (iii) reduced sensitivity to high UVR fluxes compared to autotrophic picoplankton (Callieri et al., 2001). In essence, mixotrophy functions as an energy-saving and compensatory strategy that enables these microalgae to efficiently acquire both carbon and nutrients, particularly under harmful high UVR conditions typical of these high-altitude environments (Medina-Sánchez et al., 2004).

Because of their mixotrophic nutrition mode, mixoplankton consume bacteria directly, bypassing the traditional microbial loop and limiting the development of a fully heterotrophic microbial food web. This results in the “deviated” microbial food web compared to typical oligotrophic ecosystems (Medina-Sánchez et al., 2004, 2013). By shortening the number of steps in the food web, this by-pass enhances the efficiency of energy transfer to higher trophic levels, fostering the dominance of larger zooplankton (Ward & Follows, 2016) that feed on nutrient-rich mixotrophs as a high-quality food resource (Weithoff & Wacker, 2007) and supporting a robust grazing food chain.

Mixotrophic algae also serves as potential indicators of environmental change, as their widespread presence in oligotrophic ecosystems and sensitivity to changing conditions can sig-

nal broader ecological shifts (González-Olalla et al., 2022). Observational studies in Sierra Nevada have shown that interannual environmental changes are associated with a decline in the proportion of mixotrophic algae (Carrillo et al., 2017), a reduction in algal bacterivory, and a shift toward predominantly strict autotrophic metabolism, which strengthens the commensalistic algae-bacteria relationship (González-Olalla et al., 2018). These structural and functional shifts are associated with higher mean air temperatures and increased intensity and frequency of Saharan aerosol-dust deposition, now extending into winter and spring (Carrillo et al., 2017, González-Olalla et al., 2018, Smart Ecomountains, 2022). Dust deposition increases nutrient inputs (Cabrerizo et al. 2017, Carrillo et al. 2017), yet the decline in algal mixotrophy reduces functional biodiversity and disrupts ecosystem functioning by weakening carbon transfer between mixotrophs and the grazing chain. This lowers energy transfer efficiency to higher trophic levels, potentially weakening phytoplankton–zooplankton coupling and overall grazing dynamics (Bullejos et al., 2010, Villar-Argaiz & Bullejos, 2016).

While observational approaches are valuable for assessing how communities respond to natural environmental variability, identifying the underlying abiotic drivers behind the shifts in the algae-bacteria relationship, mixoplankton prevalence, and their consequences across the trophic web has been a major challenge. To address this, a wide set of experimental approaches have been carried out in these lakes to examine how interactions among multiple global-change drivers impact algae, bacteria, and other microbes, as well as their relationship across different spatial and temporal scales (Table 1, Medina-Sánchez et al., 2022). Overall, these experiments reveal that interactions among multiple drivers strongly shapes the algae-bacteria relationship, with significant consequences for carbon flow and ecosystem functioning.

In conclusion, the combination of observational and experimental studies underscores both the complexity and sensitivity of the algae-bacteria relationship to multiple global-change drivers, establishing Sierra Nevada’s high-mountain lakes as exceptional sentinel ecosystems

for detecting and understanding environmental change.

Phytoplankton-zooplankton interactions

Interactions between zooplankton and epibiont algae: A case of mutualism

In three nearby situated Sierra Nevada lakes (greatest distance 0.5 Km), the green algae *Korshikoviella gracilipes*, an epibiont algae that attaches to zooplankton, is commonly found (Sánchez-Castillo, 1987, Pérez-Martínez & Barea-Arco, 2000, Barea-Arco *et al.*, 2001, Pérez-Martínez *et al.*, 2001). In addition to sexual reproduction, this algae also reproduces asexually through three main identified stages: zoospores, clorangioid organisms and adult organisms. The adult stage is divided into ankyroid and adult phases (Sánchez-Castillo, 1987, Barea-Arco *et al.*, 2001, Pérez-Martínez *et al.*, 2001). Each adult cell produces zoospores, but under certain conditions, adults can form cysts with resistant walls that likely overwinter in the lake sediments (Pérez-Martínez *et al.*, 2001).

In Río Seco Lake, *Daphnia pulicaria* and *Mixodiatomus laciniatus* were the main hosts for the epibiont, although *K. gracilipes* only completes its entire life cycle on *Daphnia* (the ankyroid and adult stages were found almost exclusively on this cladoceran) (Pérez-Martínez & Barea-Arco, 2000, Barea-Arco *et al.*, 2001). In consequence, the *Daphnia-Korshikoviella* interaction in this lake exemplifies similar potential host-epibiont interactions.

Pérez-Martínez *et al.* (2001) suggested that dispersal and colonization of *K. gracilipes* are highly efficient on *D. pulicaria* due to temporal synchronization between the alga's production of zoospores and cysts and the *Daphnia* moulting cycle. Zoospores, the dispersal stage, are massively released just before moulting, while cysts are released once the molts are discarded (Pérez-Martínez *et al.*, 2001). Interestingly, no correlation was found between the size of *Daphnia* and infection by *K. gracilipes* (Pérez-Martínez & Barea-Arco, 2000).

Laboratory experiments showed both negative and positive effects of *K. gracilipes* on *Daphnia*

(Barea-Arco *et al.*, 2001). Infected daphnids exhibited higher body weight and increased sinking rates, yet also higher reproductive rates compared to uninfected individuals. This increase in reproduction is attributed to *Daphnia* grazing on the large number of zoospores released by *K. gracilipes* attached to the filtering appendages of *Daphnia*. As *Daphnia* feeds on *K. gracilipes* zoospores while the algae relies on *Daphnia* for dispersal, this interaction is considered mutualistic.

Further evidence of this mutualism comes from Río Seco Lake, where Conde-Porcuna *et al.* (2014) found that the number of empty ephippia was negatively related to epibiont burden, suggesting that the amount of *K. gracilipes* (food availability) may favour an increase in the number of resting eggs per ephippium. This aligns with findings that low food availability increases the abortion of subitaneous eggs (Boersma & Vijverberg, 1995) and that most empty ephippia result from resting egg abortion (Conde-Porcuna *et al.*, 2011, see also this paper).

Phytoplankton-zooplankton coupling

The phytoplankton-zooplankton interface is essential, as it governs energy transfer and ecosystem functioning in high-mountain lakes and determines how these systems respond to environmental change. A key ecological challenge lies in disentangling how variations in food quantity and quality affect zooplankton growth and energy transfer efficiency, especially given the frequent food limitations in these oligotrophic systems. Boersma & Kreutzer (2002) challenged the long-standing belief that food quality is irrelevant in nutrient-poor environments, demonstrating that mineral limitation can occur even under extremely low food levels typical of such lakes. Despite increasing research on food quality and quantity, few studies have clearly distinguished their respective effects on consumers. Field and laboratory work in Lake La Caldera addressed this gap by systematically examining how different zooplankton taxa respond to limitations in food quantity and quality (Villar-Argaiz *et al.*, 2012). These experiments showed species-specific food quantity thresholds, with rotifers being

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the most sensitive, followed by copepods and cladocerans (Villar-Argaiz et al., 2012). In terms of food quality, P best predicted rotifer growth, while the P-normalized ω 3-polyunsaturated fatty acid index (ω 3-PUFA:P) ratio was most relevant for copepods and *Daphnia*. Subsequent studies, including Thomas (2022), reinforced these findings by demonstrating that the effects of polyunsaturated fatty acid limitation depend on P availability.

However, food quality encompasses more than elemental stoichiometry—it also refers to the overall nutritional value, composition and digestibility of phytoplankton. Studies in Sierra Nevada have driven shifts from mixotrophic to Chlorophyceae-dominated communities, likely driven by climate warming and increased nutrient inputs from dust deposition (Cabrerizo et al., 2017, Carrillo et al., 2017). Species like *Dictyosphaerium chlorelloides* can adopt bloom-growing strategies, leading to rapid nutrient uptake and decreased water transparency when zooplankton grazing fails to control algal growth. Long-term observations and mesocosm experiments indicate a growing decoupling between phytoplankton and zooplankton dynamics, leading to profound alterations in food web structure. These changes have far-reaching consequences for ecosystems, including elevated chlorophyll a, reduced water clarity, and disrupted energy flow and nutrient cycling (Villar-Argaiz & Bullejos, 2016).

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AUTHOR CONTRIBUTIONS

J.M.C.P.: Conceptualization, Writing – original draft preparation, Writing – review and editing, Visualization, Supervision. E.R.R.: Writing – review and editing. J.M.G.O.: Writing – review and editing. M.J.C.: Writing – review and editing. FP: Writing – original draft preparation, Writing – review and editing. P.C.: Writing – review and editing. J.M.M.S.: Writing - original draft preparation, Writing - review and editing. C.P.M.: Writing – review and editing. PA: Writing – review and editing. M.V.A.: Conceptualization, Writing – original draft preparation, Writing – review and editing, Visualization, Supervision.

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