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A natural history of the best studied animal groups from the Sierra Nevada watercourses

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ABSTRACT

A natural history of the best studied animal groups from the Sierra Nevada watercourses

The last 50 years of research in streams and rivers from the Sierra Nevada have provided numerous contributions that, added to the previous studies carried out in the massif, have built a great body of knowledge on particular animal groups, among other organisms. From those, Ephemeroptera, Plecoptera, Trichoptera and aquatic Coleoptera have focused the attention of the researchers in the last decades, while more recently also the brown trout has been intensely studied. The data generated from these studies have laid the groundwork for the development and implementation of biomonitoring techniques and protocols, now coordinated through the Sierra Nevada Global Change Observatory. In this article we summarize the main milestones of this period, the major findings on the biology and ecology (including recent studies on ecological stoichiometry) of these organisms and the current framework of biomonitoring, which should be maintained in the future to keep on providing data for proper management programmes. We conclude by identifying the main challenges that must be addressed to ensure the long-term conservation of stream and river fauna in Sierra Nevada.

KEY WORDS: macroinvertebrates, brown trout, mayflies, stoneflies, caddisflies, true water beetles, biomonitoring, stoichiometry, Spain

RESUMEN

Historia natural de los grupos animales mejor estudiados de los cursos fluviales de Sierra Nevada

Los últimos 50 años de investigación en arroyos y ríos de Sierra Nevada han proporcionado numerosas aportaciones que, sumadas a los estudios previos realizados en el macizo, han construido un gran cuerpo de conocimiento sobre determinados grupos animales, entre otros organismos. De ellos, efemerópteros, plecópteros, tricópteros y coleópteros acuáticos han centrado la aten-

ción de los investigadores en las últimas décadas, mientras que más recientemente también la trucha común ha sido ampliamente estudiada. Los datos generados a partir de estos estudios han sentado las bases para el desarrollo y la aplicación de técnicas y protocolos de biomonitorización, ahora coordinados a través del Observatorio del Cambio Global de Sierra Nevada. En este artículo resumimos los principales hitos de este periodo, los principales hallazgos sobre la biología y ecología (incluyendo estudios recientes en ecología estequiométrica) de estos organismos y el marco actual de la biomonitorización, la cual debería mantener en el futuro el aporte de datos que permitan la elaboración de programas de gestión adecuados. Concluimos identificando los principales retos que deben abordarse para garantizar la conservación a largo plazo de la fauna de arroyos y ríos de Sierra Nevada.

PALABRAS CLAVE: *macroinvertebrados, trucha común, efemerópteros, plecópteros, tricópteros, coleópteros acuáticos, biomonitorización, estequiometría, España.*

BRIEF HISTORICAL BACKGROUND

Sierra Nevada, due to its particular conditions, has attracted the attention of many researchers and naturalists since the last centuries, but not every ecosystem has received the same consideration. In the case of the watercourses of the Sierra Nevada (Fig. 1), the study of their aquatic macroinvertebrate fauna began at the end of the 19th century and generally corresponded to sporadic collections or inventories of captures from some scientific excursions to the massif (e.g., Rosenhauer in 1849, published in Rosenhauer, 1856).

The same trend continued in the first two thirds of the 20th century, in which some taxonomic studies were also carried out with descriptions of new species (e.g., Navás, 1902, Schmid, 1952, Aubert, 1952, 1954, Bertrand, 1954). It was in the mid-1970s and within the current Zoology Department of the University of Granada that studies began to be carried out not focusing on the inventory or taxonomy of species only, but rather on the systematized study of aspects of the biology and ecology of different groups. In that decade, Professor Fernando Jiménez Millán suggested to Javier Alba Tercedor, then a young biology student, to start studying the aquatic insect fauna of the Sierra Nevada. The first result was his degree thesis carried out in the Aguas Blancas stream (Alba-Tercedor, 1977) on the ecological factors that condition the spatial distribution of the nymphal forms of Ephemeroptera and Ple-

Figure 1. A high mountain reach of the Alhorí stream (left) and a mid altitude reach of the Andarax River (right). Photographs by M. C. Fajardo-Merlo and M. J. López-Rodríguez. *Tramo de alta montaña del arroyo Alhorí (izquierda) y tramo de altitud media del río Andarax (derecha). Fotografías de M. C. Fajardo-Merlo y M. J. López-Rodríguez.*

coptera, whose most significant results gave rise to several scientific publications (e.g., Alba-Tercedor & Jiménez Millán, 1978, Alba-Tercedor, 1979, Alba-Tercedor & Jiménez Millán, 1979). Subsequently, for his doctoral thesis he focused on the study of the taxonomy and ecology (ecological preferences and life cycles) of the nymphs of Ephemeroptera from the Sierra Nevada mountain range (Alba-Tercedor, 1981) with subsequent publications (e.g., Alba-Tercedor, 1986, 1990a), and which marked a turning point and the germ of a line of research on the streams and rivers of the Sierra Nevada that has lasted to the present day. This work was progressively joined by different researchers who have completed their doctoral theses in many cases under his supervision, and have continued this line of research. In this sense, we can highlight Antonino Sánchez-Ortega (e.g., Sánchez Ortega, 1986, Sánchez-Ortega & Alba-Tercedor, 1989, 1990) who led the study of the Plecoptera order, a line of work continued by José Manuel Tierno de Figueroa (e.g., Tierno de Figueroa, 1998, Tierno de Figueroa & Sánchez-Ortega, 1999b, 2000a), Carmen Elisa Sáinz-Cantero on aquatic Coleoptera (e.g., Sáinz-Cantero, 1989, Sáinz-Cantero et al., 1985, Sáinz-Cantero & Alba-Tercedor, 1991a, 1991b), and Carmen Zamora Muñoz on aquatic macroinvertebrate communities, biomonitoring and taxonomy of Trichoptera (e.g., Zamora-Muñoz, 1992, Zamora-Muñoz & Alba-Tercedor, 1992, Zamora-Muñoz & Alba-Tercedor, 1996). Afterwards, Pablo Jáimez Cuéllar carried out a comprehensive study of the Guadalfeo River Basin and its macroinvertebrate communities in the light of the requirements of the European Water Framework Directive (Jáimez Cuéllar, 2004), Manuel Jesús López Rodríguez studied the biology and ecology of some species of Ephemeroptera and Plecoptera from the massif (e.g., López-Rodríguez, 2008, López-Rodríguez et al., 2008) and Marta Sáinz Bariáin, who studied the effect of Climate Change on the caddisflies of the Sierra Nevada National Park (e.g., Sáinz Bariáin, 2014, Sáinz-Bariáin et al., 2016). Other animal groups have also received some attention, such as Diptera Chironomidae (e.g., Casas, 1990, Casas & Vilchez, 1992, 1993) and Nematoda (Picazo Muñoz, 1988, Ocaña et al., 1989, Ocaña & Picazo, 1991, Picazo & Ocaña, 1991) and, more punctually, turbellarians, molluscs or water mites, which have been the focus of other researchers.

Data generated during those previous decades have been used more recently, for instance, to assess the effect of the global warming on the trichopteran communities (Sáinz-Bariáin et al., 2016). By analyzing registered changes in temperature (with an average rise of 1.8ºC) on the caddisfly communities of the Sierra Nevada during a 20-year period on an altitudinal gradient range from 952 to 3050 m a.s.l., it was concluded that richness increased in altitude with maximum values at sites of intermediate-high altitude (1800–2000 m a.s.l.). The effects of the observed Climate Change may be explained by the colonization of headwaters and middle reaches from mid-lowland species or by those from streams and rivers in nearby mountain chains at lower altitude. The observed richness increased and its association with environmental conditions suggest that mountains with a considerable altitudinal gradient may function as refuges for species and populations during periods of climatic change, which strengthen the importance of the conservation of mountainous habitat.

In summary, we can affirm that the best studied fluvial macroinvertebrates in Sierra Nevada are the insects, and in particular the Ephemeroptera, Plecoptera, Trichoptera, Coleoptera (EPTC; Fig. 2) and the chironomid Diptera, with sporadic citations and descriptions of new species from other groups (see extensive review by Romero Martín & Alba-Tercedor, 2013, Ruano et al., 2013, López-Rodríguez et al., 2022).

More recently, also fish populations have been the focus of several studies. The first scientifically based results on aspects related to them in the Sierra Nevada were not obtained until the beginning of the 21st century, after some very specific work had been carried out. There were two technical commissions for the management of fishing reserves in the province of Granada (García de Jalón et al., 2003) and for the genetic characterisation of the populations of brown trout (*Salmo trutta* Linnaeus, 1758; Fig. 3) in the Sierra Nevada (although this latter is an unpublished report authored by A. Machordon in 2003, information on the genetic characterisation of the Sierra Ne-

Figure 2. Representatives of the most studied aquatic insect orders from Sierra Nevada (Ephemeroptera, Plecoptera, Trichoptera and Coleoptera). Photographs by M. J. López-Rodríguez and C. E. Sáinz-Cantero Caparrós. *Representantes de los órdenes de insectos acuáticos más estudiados de Sierra Nevada (Ephemeroptera, Plecoptera, Trichoptera y Coleoptera). Fotografías de M. J. López-Rodríguez y C. E. Sáinz-Cantero Caparrós.*

Figure 3. Brown trout from a Sierra Nevada population. Photograph by E. Sofos Naveros. *Trucha común de una población de Sierra Nevada. Fotografía de E. Sofos Naveros.*

vada populations was reported in Machordon et al., 2000). Prior to this, quotations of fish in the Sierra Nevada were based on historical documents (e.g., Madoz, 1845-1850), references from fishermen or very specific censuses for various purposes, such as the one carried out by Doadrio (2001).

In 2005, following the cataloguing of the brown trout as a species in risk of extinction in the Andalusian region (Franco Ruíz & Rodríguez de los Santos, 2001), long-term projects began, particularly the “Restoration of brown trout populations in Andalusia” and the “Andalusian fishing census”, both managed by the Regional Government. The primary objectives of these projects included the management and enhancement of knowledge regarding fish populations in Andalusia. These projects yielded highly relevant results for brown trout, particularly for populations of this species in the Sierra Nevada Mountain range. The research conducted by Sáez Gómez (2010) on the historical distribution of the species, that of Almodóvar et al. (2010) on the genetic characterisation of these trout populations, and that of Barquín et al. (2010) on the determination of the carrying capacity of the rivers in this region for the populations of this salmonid, are noteworthy, as well as their studies on ecological flows and trophic preferences of the species (Barquín et al., 2015).

Furthermore, since 2010, with the consideration of the brown trout as a quality bio-indicator within the project for the “Monitoring of the effects of Global Change in Sierra Nevada”, several lines of research, developed so far in the previously mentioned projects, have been strengthened and are currently under investigation.

Nevertheless, most of the results obtained in these projects are, to date, still relegated to what is known as “grey literature”. It was not until 2015 that part of them began to be published in scientific journals, specifically those related to the populations of brown trout in Andalusia. In chronological order, these works covered the current causes of the species' distribution in this region (Larios-López et al., 2015a), its particular reproductive phenology (Larios-López et al., 2015b), its consideration as an indicator of Global Change (Larios-López et al., 2018), the fishing modality by which it is regulated (Larios-López et al., 2019), as well as the environmental factors that regulate its population dynamics (Larios-López et al., 2021). The majority of these aforementioned investigations have been either discussed or are based on the doctoral thesis of Larios-López (2017), with all of them referring to the Sierra Nevada brown trout populations.

Finally, it is necessary to mention the publication of two fish distribution studies that included sampling points in Sierra Nevada, one at national level (Doadrio et al., 2011) and the other specific to the Guadalquivir River Basin (Fernández-Delgado et al., 2014).

In this article we summarize the main findings related to the biology and ecology of species of EPTC and the brown trout originated in studies carried out in Sierra Nevada, mainly in the last 50 years, and how they have contributed to the development of monitoring programmes in the past and that are still ongoing. Due to this wide temporal range, the scientific name of some of the species cited in the following lines have changed, so we have used the most recent nomenclature, even if in the original sources the name appears differently.

THE ECOLOGY OF STREAM ANIMALS FROM SIERRA NEVADA

In this section, we focus exclusively on studies made on the biology and ecology of aquatic animal populations in Sierra Nevada, avoiding extrapolations from studies in other areas even if they were made in species present in this mountain massif. Our focus is on the best studied taxa: four orders of aquatic insects (Ephemeroptera, Plecoptera, Coleoptera and Trichoptera) and the brown trout.

Biology and ecology of nymphs and larvae of amphibiotic insects EPT

Earlier studies on the biology of amphibiotic insects EPT date back to several decades ago, though there are still some important lagoons on several aspects of some species, mainly due to nymphs and larvae of particular species have not been described and so they are not identifiable. First articles focused on the ecological factors determining the distribution of species within some stream reaches (e.g., Alba-Tercedor, 1977, Alba-Tercedor & Jiménez Millán, 1978, Alba-Tercedor, 1979, Alba-Tercedor & Jiménez Millán, 1979, Sánchez-Ortega & Alba-Tercedor, 1989, Zamora-Muñoz et al., 1993). Further data obtained from a particular stream showed that for both mayflies and stoneflies, flow (measured in the bottom), the nature of the substrate and the vegetation mostly conditions the distribution of species (Alba-Tercedor & Jiménez Millán, 1978, Alba-Tercedor, 1979). This was later supported by Sánchez-Ortega & Alba-Tercedor (1989) in stoneflies, who found different species were distributed differently depending on flow, substrate and vegetation, and according to temperature preferences. Further studies in the Río Monachil, affected by sewage discharges next to its source due to the presence of the ski resort, showed that different factors, apart from organic pollution, affect at different species of mayflies and stoneflies, among which the most common are water temperature, oxygenation and mineralization (Zamora-Muñoz et al., 1993).

These studies were the base for further research on the life cycle of particular species, mainly on Ephemeroptera and Plecoptera initially, with the doctoral thesis of Alba-Tercedor (1981) and Sánchez-Ortega (1986), and later on with the one of López-Rodríguez (2008), but also on Trichoptera more recently with the doctoral thesis of Sáinz-Bariáin (2014).

First studies, and some later ones, focused on the life strategies of mayflies, and detected that the most prevalent life cycles in the Sierra Nevada species are univoltine (e.g., Alba-Tercedor, 1990a, 1990b, Alba-Tercedor & Derka, 2003), with particular species having a semivoltine life cycle (*Ephemera danica* Müller, 1764; Alba-Tercedor, 1990a), and others with bivoltine or even possibly trivoltine cycles [e.g., *Baetis alpinus* (Pictet, 1843), *B. maurus* Kimmins, 1938, *Alainites muticus* (Linnaeus, 1758) or *Centroptilum luteolum* (Müller, 1776); Alba-Tercedor, 1983, 1986, López-Rodríguez et al., 2008]. For many of these species, asynchronous hatching seems to be relatively common [e.g., *Baetis rhodani* (Pictet, 1843), *B. maurus*, *Epeorus sylvicola* (Pictet, 1865)/*E. torrentium* Eaton, 1881, *E. danica*, *Serratella ikonomovi nevadensis* (Alba-Tercedor, 1983); Alba-Tercedor, 1983, 1986, 1990a, 1990b]. In some cases, this is reflected in a relatively expanded emergence period, as in *E. danica*, but not always, as occurs in *Oligoneuriella marichuae* Alba-Tercedor, 1983 (Alba-Tercedor, 1990a, 1990b). Nonetheless, this asynchrony in hatching seems to be population specific, and probably depending on ecological factors, as more recent studies in previously studied species have not found it [e.g., *S. ikonomovi nevadensis* (López-Rodríguez et al., 2008)]. Also changes in voltinism have been recorded in Sierra Nevada in the same species at different altitudes, as in the case of *A. muticus*, which shows a univoltine cycle at 1540 m a.s.l and a bivoltine one at 1840 m a.s.l., or changes in the developmental period, as for *Ephemerella ignita* (Poda, 1761) or *S. ikonomovi nevadensis* (López-Rodríguez et al., 2008). For several mayfly species, these studies showed different strategies in comparison to different European populations, while the life cycle of some others was similar to that found in other high-altitude mountains (Bauernfeind & Soldán, 2012). This underlines the similarities between Sierra Nevada and other high, temperate mountains, and also the particularities of being the southernmost mountain range with those high altitudes under a mostly Mediterranean climate.

Compared to mayflies, stoneflies seem to have less variable life cycles in Sierra Nevada, and changes in voltinism have not been detected in the populations inhabiting the mountain range. In particular species, there seems to be an effect of temperature on the developmental period, as recorded in *Protonemura meyeri* (Pictet, 1841) by Sánchez-Ortega & Alba-Tercedor (1990), but this is not so intense as in mayflies. Most species present in Sierra Nevada have a univoltine life cycle (e.g., Sánchez-Ortega & Alba-Tercedor, 1988, 1990, López-Rodríguez et al., 2008, 2012), but two of them, belonging to the Pelidae family, namely *Perla marginata* (Panzer, 1799) and *Dinocras cephalotes* (Curtis, 1827), have a merovoltine, probably three-years long, life cycle (Sánchez-Ortega & Alba-Tercedor, 1991). Possibly also the recently described *Perla andalusiaca* Reding, 2023 has a similar strategy. Nonetheless, the exact duration of the nymphal development period should be studied in other populations of the massif, as in some of these species, variations in its length have been recorded at different latitudes in relation with differences in temperature (e.g., Frutiger, 1987, Sand & Brittain, 2001, Tierno de Figueroa et al., 2015).

In Sierra Nevada, the life cycles of caddisflies have not been as thoroughly studied as those of mayflies and stoneflies over time. Only the life history of *Stenophylax nycterobius* (McLachlan, 1875), *Annitella iglesiasi* González & Malicky, 1988 and *A. esparraguera* Schmid, 1952 have been analysed within the massif (Sáinz-Bariáin & Zamora-Muñoz, 2012, Sáinz-Bariáin, 2014). The species *S. nycterobius* has been found inhabiting headwater streams from 1704 to 3050 m a.s.l. (Sáinz-Bariáin & Zamora-Muñoz, 2012), above the limits recorded as preferential for this species in other European ecoregions (*sensu* Graf et al., 2008). In the analysed population, the life cycle was univoltine, as in other regions, but with some phenological variations (Sáinz-Bariáin & Zamora-Muñoz, 2012). This univoltine strategy was found also in the other two studied species, *A. iglesiasi* and *A. esparraguera*, analysed at different altitudes (Zamora-Muñoz et al., 2012, Sáinz-Bariáin, 2014, Múrria et al., 2020). In these two species, differences in the timing of emergence and the developmental rate were detected in relation with altitude, starting the emergence before at higher altitude. Sáinz-Bariáin (2014) also found correspondences between the life history of these species at high altitudes in Sierra Nevada and the life history of a close related species, *Annitella obscurata* (Mclachlan, 1876) in Norway, supporting similarities between the nevadensis massif and upper latitude regions. So, at these lower latitudes, species find at higher altitudes conditions like those occurring at higher latitudes. This is especially important in cold stenotherm species under the current Climate Change framework, that would need to migrate either in latitude or in altitude to mitigate the effect of increasing temperature. In this sense, the headwaters of Sierra Nevada would act as climatic refuges for aquatic insects. This has been demonstrated in the communities of caddisflies from Sierra Nevada (Sáinz-Bariáin et al., 2016), as reported above. Regarding the species that are already relatively isolated in the peaks of Sierra Nevada, increasing temperatures and subsequent environmental changes may affect their populations in the massif. In fact, in a space-for-time approach using the mayfly *B. alpinus* as species model in recently deglaciated mountains, Finn et al. (2014) predicted that genetic diversity of the species can suffer significant losses and that entire species are likely to be lost from these uppermost tips of stream networks due to decreasing influence of glaciers on stream hydrology. Thus, this could occur also in many other aquatic insect species from high mountain streams as, for instance, the endemics *P. andalusiaca* or *Limnephilus obsoletus* Rambur, 1842 (Tinaut et al., 2024).

A key factor affecting nymphs and larvae is diet. Feeding ecology affects the growth rate and development of the immature stages and also has an effect on the food web of the entire stream community. This is particularly important in the case of species at the top of the food web, such as some stoneflies belonging to the Perlidae family, which act as the main macroinvertebrate predators in these streams, in some cases together with Odonata. The diet and trophic behaviour of several species have been studied in Sierra Nevada populations, mainly in stoneflies and mayflies, but also in some caddisflies. Within the EPT taxa we find representatives of every main functional feeding group (FFG) *sensu* Cummins (1973), though filterers have not been studied at the species level, but at the genus level (Tierno de Figueroa et al., 2019).

Within predators, information on the diet of four species is available from Sierra Nevada populations, namely *P. marginata*, *Perlodes microcephalus* (Pictet, 1833), *Isoperla nevada* Aubert, 1952 and *Rhyacophila nevada* Schmid, 1952 (Bello & Alba-Tercedor, 2004, López-Rodríguez et al., 2012, Tierno de Figueroa et al., 2019). In the case of stoneflies, the perlid *P. marginata* was studied in several streams at different altitudes from four different basins of the mountain range and it showed a great variability in diet, also incorporating non-animal matter in some populations (Tierno de Figueroa et al., 2019). In a high mountain reach, *P. microcephalus* acted as a more voracious predator than *I. nevada*, and both incorporated also non-animal matter to their diet, being generalists. The former had a wider prey spectrum than the latter that included Chironomidae, stoneflies, mayflies and caddisflies, among others, in comparison with *I. nevada*, which fed only on Chironomidae, stoneflies and mayflies (López-Rodríguez et al., 2012). Also *R. nevada* seems to feed on several different prey, such as Chironomidae, mayflies and caddisflies, and differences in their proportion and importance in the diet were found when comparing a population upstream and downstream of a big reservoir in the upper part of the Genil River, the Canales reservoir (Bello & Alba-Tercedor, 2004).

Both mayflies and stoneflies are represented among the collector-gatherers FFG, of which the mayflies *E. ignita*, *S. ikonomovi nevadensis*, *A. muticus*, *B. alpinus* and the stonefly *Amphinemura triangularis* (Ris, 1902) have been studied in Sierra Nevada (López-Rodríguez et al., 2008). The organic detritus is the main component of the diet of these species, but other resources are also used, as diatoms, fungi, pollen or moss phyllidia. In the case of *B. alpinus*, a switch in its feeding functional role to mainly scraper was reported in a population at lower altitude, in comparison with a higher altitude population. Nonetheless, in all these species, variability in the diet was detected. *Capnioneura mitis* Despax, 1932 is the only studied species in Sierra Nevada that has been classified mainly as shredder, though also had, at low altitude, an important function as scraper (López-Rodríguez et al., 2008). All these species (*E. ignita*, *S. ikonomovi nevadensis*, *A. muticus*, *B. alpinus*, *A. triangularis* and *C. mitis*) showed ontogenetic changes in their diet, in most cases decreasing the ingestion of detritus and increasing the amount of other resources such as diatoms or phyllidia, or, as occurring in other species such as *R. nevada*, increasing the number of prey ingested when bigger (Bello & Alba-Tercedor, 2004).

Other taxa have been studied at the genus level in a comparative analysis of their diet in four different basins from Sierra Nevada, at three different altitudes and in two seasons, showing remarkable changes in their feeding behaviour, and so in their functional role, depending on the site, the availability of food sources and conditions (Tierno de Figueroa et al., 2019). For instance, the caddisfly *Hydropsyche* sp. acted as collector-filterer, predator, scraper or even shredder in some sites, *Micrasema* sp. behaved as collector-gatherer, scraper or shredder, and the mayflies *Epeorus* sp. and *Baetis* sp. were classified as both collector-gatherers and scrapers.

All these results showing the variability of feeding habits of taxa stress the need for detailed studies in particular populations and sites, and under different conditions, as well as the caution researchers must have when assuming trophic roles of species in food web analyses.

A physiological aspect related with the fitness of particular populations is the enzymatic antioxidant potential. This has been studied in three species from Sierra Nevada, such as *E. danica*, *P. marginata* and *Isoperla grammatica* (Poda, 1761), as well as in others present in the massif but studied out of it, such as *D. cephalotes* and *Hydropsyche* spp. (Sanz et al., 2010, 2017). These results showed that the enzymatic antioxidant potential of the *P. marginata* and *I. grammatica* could help them to withstand with adverse conditions in the framework of current Climate Change, though in *E. danica* from a low altitude stream reach the values of antioxidant capacity were the lowest of all the species compared, and the second greatest regarding oxidative damage, so showing a high oxidative imbalance (Sanz et al., 2017). This could make it especially vulnerable to disturbances, both short and long term.

Though several factors may act as stimulus for particular life cycle or phenological events, such as temperature, diet and photoperiod (Sweeney, 1984), only the effect of light has been studied in certain species of stoneflies from Sierra Nevada (Tierno de Figueroa & Sánchez-Ortega, 2000b), showing the preference of most of them, especially *C. mitis*, for nocturnal emergence. This would reduce the effect of predators on them, such as birds or other arthropods, so this strategy could be widespread among stoneflies. In mayflies and caddisflies, there are no studies on the factors triggering the pass to the terrestrial ecosystem.

Biology and ecology of adult amphibiotic insects EPT

The studies on the ecology and biology of EPT during their terrestrial stage in Sierra Nevada are relatively scarce in comparison with those taxonomical and faunistic, or even with the studies on the ecology and biology of nymphs and larvae. This lack of knowledge makes difficult to understand the complex ecological relationships established between the river environment itself and the riparian zone, where the adults of these insects carry out part of their lives, which implies a continuous flow of matter and energy between both environments through the emergence of adults, in one direction, and the laying of eggs and death (mainly of the females after oviposition), in the opposite direction.

One important aspect of the role of these insects in the terrestrial environment is their trophic ecology. In Sierra Nevada, this aspect has been studied only in the case of stoneflies, where the feeding habits of 16 species have been described in different streams and rivers (Tierno de Figueroa & Sánchez-Ortega, 1999b, 2000a). Those studies were pioneered for this animal group as a global scale because they considered also the diet variation along the flight period, showing that different species differs in the importance of the ingested items (pollen of Poaceae, Pinaceae, etc., fungi hyphae and spores, cyanolichens, fine particulate organic matter, coarse particulate organic matter...) and, also, that the diet change along the flight period depending of the resource availability in some species but not in others. These studies also highlighted that feeding in adult Plecoptera was more important than previously thought, as only in the large-size species (*P. marginata* in these studies) adults appear to survive primarily on reserves accumulated during the nymphal stage (Tierno de Figueroa & Sánchez-Ortega, 1999b, 2000a). One important aspect not yet evaluated in this area is the role of the different species of stonefly adults and other amphibiotic insects in the diet of terrestrial predators such as spiders, birds, etc., as demonstrated in a few other places (e.g. Collier et al., 2002), being part of the terrestrial food webs (Tierno de Figueroa & López-Rodríguez, 2019). There are no studies on the adult feeding of the Ephemeroptera and Trichoptera in Sierra Nevada, although it is expected that Ephemeroptera species do not feed at all during their sub-imaginal and imaginal stages, as is the rule for this insect group with vestigial mouthparts in the winged stages (Sartori & Brittain, 2015), while Trichoptera species probably only ingest water and nectar (Holzenthal et al., 2015).

Published phenological studies on adults of amphibiotic insects in Sierra Nevada are mainly available for Plecoptera (e.g. Sánchez-Ortega & Alba-Tercedor, 1989, Tierno de Figueroa et al., 2001), although data on adult captures of different groups (Ephemeroptera, Trichoptera, etc.) are common in taxonomic and faunistic works (see Ruano et al., 2013 and references herein) as well as in the dataset coming from the Sierra Nevada Global Change Observatory's long-term monitoring data (see section on biomonitoring below). Recently, the compilation of López-Rodríguez et al. (2024) provided a very valuable information useful for knowing the flight periods of Plecoptera and Trichoptera in Sierra Nevada, as well as the period of the year in which adult Coleoptera are present.

Studies on life cycles and life histories (addressed before, in the section dedicated to nymphs and larvae) also provide valuable information on the emergence date and flight periods of EPT taxa in Sierra Nevada. For example, an interesting study on the caddisfly *S. nycterobius* life history in this massif showed that adults emerged in September and that, contrary to what happens in other areas, they not migrated into caves for undergoing a summer diapause before mating, but they mate and lay eggs immediately after emergence when the waters of the streams are not yet frozen (Sáinz-Bariáin & Zamora-Muñoz, 2012). Zamora-Muñoz et al. (2012) pointed out that *L. obsoletus* presents a spring or early summer emergence, while the two species of *Annitella*, *A. esparraguera* and *A. iglesiasi* have an autumn or late summer emergence, with a more delayed emergence in lower altitude streams. For Ephemeroptera, there is also information on the emergence of many species obtaining from the study of their life cycles, such as the case of *O. marichuae* with a short emergence period beginning in late August, *S. ikonomovi nevadensis* with emergences between mid-June and mid-August, *Torleya nazarita* Alba-Tercedor & Derka, 2003 with a flight period during June (Alba-Tercedor, 1990b), or of the polyvoltine species of the genera *Baetis* and *Centroptilum* with more than one emergence period in different seasons (Alba-Tercedor, 1986) (see more information in the section on biology and ecology of nymphs and larvae).

Sánchez-Ortega & Alba-Tercedor (1989) noted that most of the stonefly species in Sierra Nevada, from 19 studied species, emerged along two seasons. Although adults of different species can be found all along the year, the most common emergence period was the spring-summer one, that is the typical flight period of all the species with long life cycles (merovoltines), such as *D. cephalotes* and *P. marginata*, and some of the univoltine species. The presence of adults during all the seasons makes them particularly important for some predators like birds in terrestrial environments, mainly in the cold seasons, when many other insects are scarce or inexistent. From data collected in the field, Tierno de Figueroa et al. (2001) studied in detail the phenology of several different populations of 16 stonefly species, cataloguing them in seven groups according to their flight period and confirming grosso modo previous results (Sánchez-Ortega & Alba-Tercedor, 1989). Three species (*Protonemura alcazaba* (Aubert, 1954), *P. meyeri* and *C. mitis*) showed an extended flight period, i.e., spreading during three seasons. Particularly interesting was the study of the intraspecific variations in flight periods between rivers in relation to water temperature, showing that the emergence of some species was clearly conditioned by the water temperature while in other species the photoperiod was the main conditioning with independence of the detected differences on water temperature. In this study, a clear temporal separation or segregation was observed in the flight periods, or at least in their maxima, of the different species of the genus *Leuctra* Stephens, 1836 (the most diverse stonefly genus in Sierra Nevada). This temporal segregation between related species, previously observed in other aquatic insects (including other stonefly taxa) from other areas, may be an important reproductive isolation mechanism and minimize the interspecific competition (Tierno de Figueroa et al., 2001 and references herein). The intraspecific differences in flight periods in relation to the sex have been also studied in 11 stoneflies species (Tierno de Figueroa et al., 2003), quantifying them with the help of a protandry index (that indicate the displacement of the flight period of the female in relation to that of the male and ranging from -1 to 1) and showing protandry values ranging between 0.07 and 0.33. Those results indicated a relatively advance of the flight period in males (less pronounced in species with extended or very time-concentrated flight periods). Protandry is important ensuring that males are ready for mating when females begin to be available. No significant correlation was detected between protandry degree and sexual size-dimorphism degree, contradicting the theoretical expectations (Tierno de Figueroa et al., 2003 and references herein). The study of different populations of 12 stoneflies species from Sierra Nevada showed that average size of individuals decreased throughout the entire flight period in all species studied except those with an extended flight period (Tierno de Figueroa & Sánchez-Ortega, 2004). This fact could indicate that individuals that emerge at the beginning of the flight period are those with an optimal growth, while those that did not reach an optimal size should delay the emergence but constrained by their innate propensity to undergo metamorphosis during a specific time of the year, as suggested by some authors in different aquatic insect groups (Tierno de Figueroa & Sánchez-Ortega, 2004).

Adults of most of the amphibiotic insects use to occupy the riparian habitat and close areas, where they can remain on the rocks, on or hidden in the vegetation or flying, sometimes forming aerial swarms (the latest is common to Ephemeroptera, many Diptera and Trichoptera, etc.) or defending their territories (Odonata, some Diptera) (Tierno de Figueroa, 2000, Lancaster & Downes, 2013). In Sierra Nevada, a study on adults of two stonefly species (Plecoptera) and one caddisfly species (Trichoptera), showed that they exhibited three different strategies regarding the spatial distribution patterns on the riparian vegetation: *I. nevada* showed a contagious distribution, probably related to the existence of aggregation sites for mating or feeding, *Chloroperla nevada* Zwick, 1967 showed an aleatory distribution, as expected in this species that has a relatively higher mobility, and *Sericostoma* cf. *vittatum* Rambur, 1842 showed a random and pair-wise distribution probably as consequence of the existence of a mate-guarding mechanism or the transference of additional material together with sperm (Tierno de Figueroa et al., 2000).

Although it has been repeatedly observed in different mayfly species from Sierra Nevada, no studies have been developed on the swarming of these species. They carry out these swarms to attract females, which will enter the swarms and, after mating with a male, abandon it to lay their eggs in the water (Sartori & Brittain, 2015). Together with the existence of mating aggregating sites, stoneflies use to employ an intersexual vibrational communication system (with species specific signals produced by drumming, rubbing, tremulation or a combination of these methods) stablishing male and female duet that favour the mate encounter and female mate election (Stewart, 1994, Tierno de Figueroa et al., 2019). In Sierra Nevada, the drumming signal of three species have been described: *I. nevada*, *P. meyeri* and *C. mitis* Despax, 1932 (Tierno de Figueroa & Sánchez-Ortega, 1999c, Tierno de Figueroa et al., 2009, 2014). The male signal of *I. nevada* is a complex group of diphasic sequences (the first one different to the others) composed by many beats (Tierno de Figueroa & Sánchez-Ortega, 1999c), while the male drumming signal of *C. mitis* is simple, consisting of a repetition of beats with an almost constant inter-beat duration, being a monophasic signal relatively simple (Tierno de Figueroa et al., 2009). The male drumming signal of *P. meyeri* has an intermediate complexity and it consists of a repetition of 3 to 11 monophasic sequences of a few beats each one, while the female signal is a long repetition of 5 to 109 beats (Tierno de Figueroa et al., 2014). The study of mating behaviour of different species of stoneflies from Sierra Nevada (Tierno de Figueroa, 2003) has shown that the existence of mate guarding (by the male remaining in the mating position) is common in this insect group, and that in some species the mate guarding is considerably delayed when displacement attempts by other males occur (for example in *Leuctra fusca* (Linnaeus, 1758)) while in other species the duration is fairly constant independently of the existence of displacement attempts (e.g. *Leuctra andalusiaca* Aubert, 1962). This study also demonstrated, contrary to previous general assumptions, that females of some stonefly species could copulate more than once and evidenced that the mating is complex and diverse within this animal group (Tierno de Figueroa, 2003). Regarding Trichoptera, described mating strategies at global scale are very diverse, including the use of sexual pheromones (e.g. Wood & Resh, 1984), the vibrational signals (e.g. Ivanov, 1994), the visual detection of distinctive flight patterns and swarming (Holzenthal et al., 2015, Morse et al., 2019), etc., for mate encounter and pair election. Copulations occur on vegetation or on the ground, sometimes inside the swarm, with males transferring sperm freely or in a spermatophore; multiple copulation by females and males as well as sperm displacements by other males have been also described in some species (Holzenthal et al., 2015, Morse et al., 2019). Unfortunately, no studies have been carried out on any caddisfly species on these interesting aspects of their adult biology in Sierra Nevada.

Information of main oviposition behaviours of Ephemeroptera, Plecoptera and Trichoptera is compiled in some reviews on this insect orders such as those of Sartori & Brittain (2015) for mayflies, DeWalt et al. (2015) for stoneflies and Holzenthal et al. (2015) for caddisfly, and general data on lifelong fecundity (number of eggs per female), together with information adult life span and other traits, for many European genera is available in the database of Sarremejane et al. (2020). In Sierra Nevada, Tierno de Figueroa & Sánchez-Ortega (1999a) supported a valuable information on the egg and clutches of 16 stonefly species, e.g. the maximum fecundity is variable among species, oscillating between less than 100 to more than 1500 eggs, with higher fecundity in the larger species but with some exception to this rule, the female can produce a few clutches with or without copulation between them, the egg mass is transported at the end of the abdomen and the oviposition occur with females introducing the apex of the abdomen in water and releasing the eggs either by making short flights (e.g. *P. marginata* or *L. fusca*) or by skating on the water surface (e.g. *P. meyeri* or *Leuctra iliberis* Sánchez-Ortega & Alba-Tercedor, 1988). Afterwards, Tierno de Figueroa & López-Rodríguez (2005) studied the relationship among female size, fecundity, egg mean size and flight period in a population of *I. nevada* from Sierra

Nevada, demonstrating that the female size is a good indicator of its reproductive potential. So, bigger females, which emerge at the beginning of the flight period produce the greater number of eggs (although no difference in the egg size was detected) (Tierno de Figueroa & López-Rodríguez, 2005). Regarding caddisflies, Sáinz-Bariáin (2014) noted that *Annitella iglesiasi* and *A. esparraguera* mate immediately after emergence, that, in laboratory conditions, females laid the eggs just after the mating, and that egg hatching occurred five weeks after the egg-laying.

Biology and ecology of the true water beetles

Although the aquatic Coleoptera fauna of the Sierra Nevada is one of the best known on the Iberian Peninsula (Sáinz-Cantero, 2013), studies on the biology and ecology of the populations of the Sierra Nevada are very scarce, especially with regard to those that inhabit its running waters (headwater streams, mountain rivers, irrigation channels, irrigation ditches), for which most of the data are very scattered in publications of various kinds (faunistic, taxonomic or conservation, for instance).

The contributions that specifically explore the environmental factors that determine the distribution of fluvial species or their phenology are those by Sáinz-Cantero (1985) and Sáinz-Cantero et al. (1985, 1987, 1988), referring to eight rivers of the western end of the massif, as well as Sáinz-Cantero (1989) and Sáinz-Cantero & Alba-Tercedor (1991a, 1991b), in this case based on data collected in a hundred localities widely distributed throughout the Sierra Nevada.

According to the information provided by these studies, Coleoptera communities are structured in relation to the wide altitudinal gradient existing in the area (Sáinz-Cantero, 1989, Sáinz-Cantero & Alba-Tercedor, 1991a, 1991b) and show that only a very small number of species inhabit altitudes above 2500 m a.s.l. where environmental conditions are extremely severe (low thermal stability, high irradiation, short dry seasons and low nutrient levels). These are mainly generalist species that also occur in ponds or other standing water environments and tolerate wide ranges of temperature, pH and conductivity, such as *Dryops gracilis* (Karsch, 1881), *Haliplus lineatocollis* (Marsham, 1802), *Anacaena globulus* (Paykull, 1798) or *Agabus bipustulatus* (Linnaeus, 1767), considered as ubiquitous species (e.g., Bilardo, 1969, Ravizza, 1972, Van Berge Henegouwen, 1986, Ribera et al., 1988), and even *Limnebius truncatellus* (Thumberg, 1794) a species that in Sierra Nevada shows considerable ecological plasticity (Sáinz-Cantero & Alba-Tercedor, 1991b). An exception is the Iberian endemic *Helophorus nevadensis* Sharp, 1916 and *Helophorus glacialis* A. Villa & G. B. Villa, 1833 (considered as a glacial relict species by Angus, 1985) which have always been found in environments with poor substrates in bases and very little mineralised water (Sáinz-Cantero, 1989, Sáinz-Cantero & Alba-Tercedor, 1991b).

The rest of the species are distributed below 2200 m a.s.l., where environmental conditions are more favourable and include areas with more heterogeneous geological characteristics than in the previous altitudinal range. These communities are dominated by typically rheophilous species and, as part of them, most of the Iberian endemisms found in the massif (Sáinz-Cantero, 2013). Most of them show wide tolerance ranges with respect to temperature, pH, current velocity or degree of mineralisation of the water and are found in a variety of environments: from watercourses with considerable flow to shallow streams with weak current, irrigation canals or sewage ponds (e.g., *Hydroporus discretus* Fairmaire, 1859, *H. lucasi* Reiche, 1866, *Elmis maugetii* Latreille,1798, *Limnius volckmari* Panzer, 1793, or *Hydraena capta* Orchymont, 1936).

However, some show a certain preference for particularly cold waters, such as *Agabus guttatus* (Paykull, 1798) or the endemic *Hydrochus nooreinus* Berge Henegouwen & Sáinz-Cantero, 1992 and *Nebrioporus bucheti cazorlensis* (Lagar, Fresneda & Hernando, 1987) (Sáinz-Cantero, 1989, Sáinz-Cantero & Alba-Tercedor 1991a, 1991b), while others prefer more or less mineralised aquatic environments, depending mainly on the lithological characteristics of the substrate within this altitudinal range. Thus, species such as *Oreodytes davisii* Curtis, 1831 or the endemic *Deronectes depressicollis*

(Rosenhauer, 1856) (Sáinz-Cantero, 1989, Sáinz-Cantero & Alba-Tercedor, 1991a) are mainly found in the predominantly siliceous zone of the Sierra Nevada, where running waters have a low degree of mineralisation and are poor in bases. Others, on the contrary, restrict their presence to the limestone rim bordering the massif on its northwestern and southern slopes, where the waters are more mineralised and richer in bases. Among these species, some show significant preferences for the high values of conductivity typical of calcareous headwaters (Sáinz-Cantero, 1985, Sáinz-Cantero et al., 1985, 1987), such as the Iberian endemic *Hydraena tatii* Sáinz-Cantero & Alba-Tercedor, 1989, *Hydraena carbonaria* Kiesenwetter, 1849, *Hydraena quilisi* Lagar, Fresneda & Hernando, 1987 or the representatives of the genus *Riolus* Mulsant & Rey, 1872.

There are no specific studies on the life cycles of the populations of nevadensis aquatic Coleoptera, probably due to the difficulty of taxonomically identifying their larval stages, whose distinctive characteristics have not been described for most of the species found in the massif. However, the works of Sáinz-Cantero (1985) and Sáinz-Cantero et al. (1987, 1988) provide an approximation to the phenology of some fluvial species located in the extreme northwest, based on the presence/absence of adults or, in the Monachil river, of adults and larvae.

An ecological stoichiometry perspective on aquatic insects

Ecological stoichiometry looks at how the nutrient makeup of things like plants or dead organic matter can vary a lot, while animals and other consumers usually keep a steadier, balanced internal nutrient composition (Sterner & Elser, 2002). Viewing trophic interactions as a balance -or imbalance- of elemental exchanges helps us understand how nutrient makeup influences growth, nutrient cycling, and energy flow. This perspective can improve our ability to predict things like nutrient limitation, competition for resources, and how ecosystems respond to environmental changes. A study of major rivers in the Sierra Nevada (Genil, Dílar, Trevélez and Poqueira), spanning an altitudinal gradient from headwaters to lower reaches, revealed notable variation in elemental composition across 12 aquatic insect taxa (Fig. 4). Carbon (C) content ranged between 44% and 54% of dry weight, and nitrogen (N) from 7% to 12%, while phosphorus (P) exhibited much greater variability, ranging from 0.4% to 1.1% of dry weight (Villar-Argaiz et al., 2020). These results align with previous studies reporting C content between 40-50% and N content around 10% (e.g., Back & King, 2013). Strikingly, results of Villar-Argaiz et al. (2020) showed up to a three-fold difference in the P content among taxa. When quantified using the coefficient of variation (CV), P displayed nearly twice variability of C and N (e.g., CV for P = 27% vs. C = 14%) (Villar-Argaiz et al., 2020). Collectively, these results indicate that P, rather than C or N, primarily drives differences in C:N:P ratios among benthic macroinvertebrates, consistent with other studies (Frost et al., 2005 and references therein).

One of the most compelling questions in ecological stoichiometry is then what drives variation in elemental composition among animals, particularly in P, the most variable of essential elements. Data from the Sierra Nevada corroborate findings from the extensive StoichLife dataset (González et al., 2025), showing that body mass is a weak predictor of interspecific variation in P content, while taxonomic identity plays a more significant role. However, it has been also observed that variation in elemental composition within taxa is comparable to -or even exceeded- that among taxa, highlighting the significant influence of ontogeny on stoichiometric patterns. As with taxonomic differences, much of this ontogenetic variability was driven by changes in phosphorus (P) content. Most intriguingly, patterns of P content across development differed between hemimetabolous and holometabolous insects (Fig. 5). For instance, in the holometabolous *Hydropsyche* sp., P content declined with increasing larval size, whereas in the hemimetabolous *Dinocras cephalotes*, P content increased with body size during nymphal development. These findings suggest that developmental mode can shape the relationship between body size and phosphorus content, potentially revealing evolutionary life history strategies related to nutrient demands,

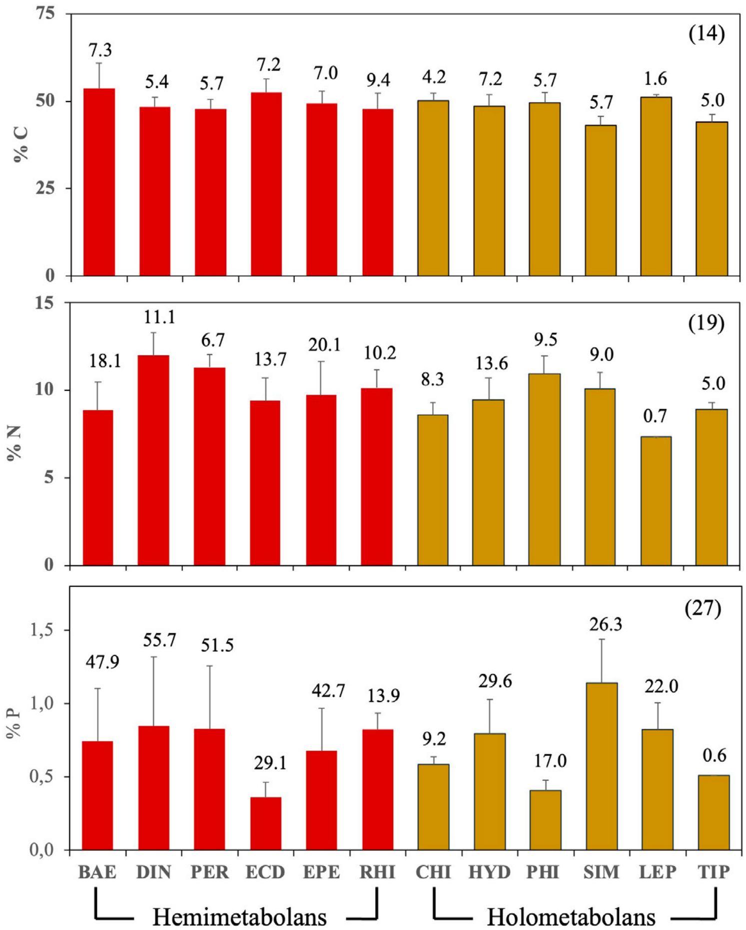

Figure 4. C:N:P stoichiometry of macroinvertebrate taxa analyzed from data in Villar-Argaiz et al. (2020) and unpublished data. Values are presented as means ± standard deviation (SD). Coefficients of variation (CV) for C, N, and P content are shown as intraspecific values (above each column) and interspecific values (in parentheses). Taxa abbreviations: BAE – *Baetis* sp.; CHI – Chironomidae; HYD – *Hydropsyche* sp.; PHI – *Philopotamus* sp.; SIM – Simuliidae; DIN – *Dinocras cephalotes*; PER – *Perla marginata*; EPE – *Epeorus* sp.; LEP – Lepidostomatidae; RHI – *Rhithrogena* sp.; TIP – Tipulidae. *Relaciones estequiométricas C:N:P de los taxones de macroinvertebrados analizados a partir de datos de Villar-Argaiz et al. (2020) y datos no publicados. Los valores se presentan como medias ± desviación estándar (DE). Los coeficientes de variación (CV) para el contenido de C, N y P se muestran como valores intraespecíficos (sobre cada columna) e interespecíficos (entre paréntesis). Abreviaturas de los taxones: BAE:* Baetis *sp.; CHI: Chironomidae; HYD:* Hydropsyche *sp.; PHI:* Philopotamus *sp.; SIM: Simuliidae; DIN:* Dinocras cephalotes*; PER:* Perla marginata*; EPE:* Epeorus *sp.; LEP: Lepidostomatidae; RHI:* Rhithrogena *sp.; TIP: Tipulidae.*

particularly for phosphorus, which is essential for growth. In an analysis of nucleic acid content from 639 macroinvertebrate specimens from the Sierra Nevada, we found that %RNA -a phosphorus-rich molecule commonly used as a proxy for growth- was especially high during early developmental stages in holometabolous larvae (Villar-Argaiz et al., 2021). This pattern suggests an evolutionary adaptation favoring rapid growth in holometabolans compared to hemimetabolans. Furthermore, the significant interaction between body length and metamorphosis mode for both RNA content and RNA:DNA ratio provides strong evidence for an ontogenetic component in RNA allocation.

In summary, studies in the Sierra Nevada reveal that ontogenetic shifts in elemental composition are substantial and may have important, yet still poorly understood, ecological consequences. These could include effects on growth and nutrient limitation, particularly when the elemental demands of developing organisms are not met by the available resources, potentially leading to population bottlenecks and broader ecosystem impacts.

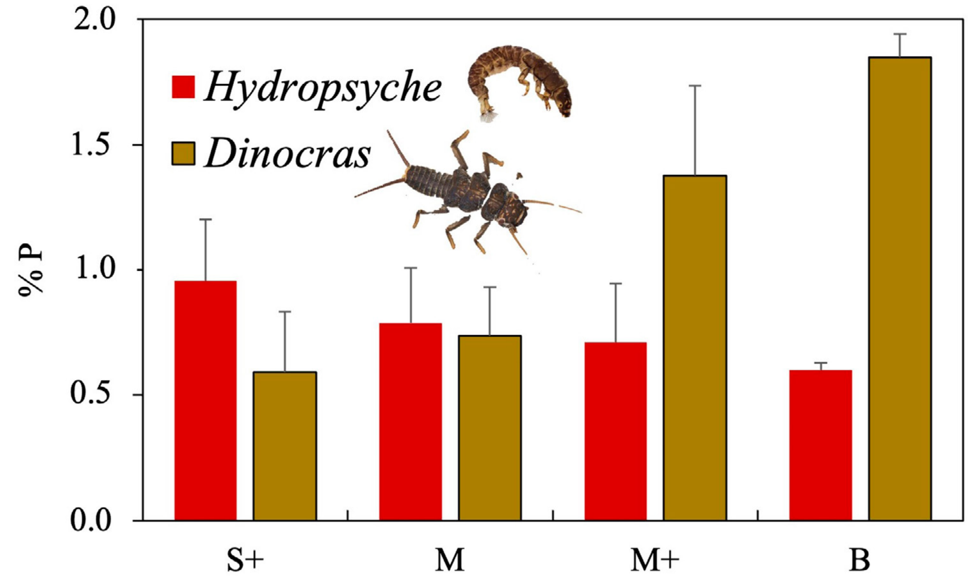

Figure 5. Phosphorus content across size classes in the holometabolous *Hydropsyche* sp. and the hemimetabolous *Dinocras cephalotes*. Individuals were grouped into quartile size categories based on the smallest and largest body masses observed for each taxon: small (S), medium (M), medium+ (M+), and big (B). *Contenido de fósforo por clases de tamaño en el holometábolo* Hydropsyche *sp. y el hemimetábolo* Dinocras cephalotes*. Los individuos se agruparon en categorías de tamaño por cuartiles basadas en las masas corporales más pequeña y más grande observadas para cada taxón: pequeño (S), mediano (M), mediano+ (M+) y grande (B).*

Biology and ecology of the brown trout

The natural fish communities of the Sierra Nevada massif are characterised by the exclusive presence of the common trout (*Salmo trutta* Linnaeus, 1758) in the upper reaches of its rivers. The progressive increase in temperature downstream makes it possible for this salmonid to coexist with the native Andalusian barbel (*Luciobarbus sclateri* (Günther 1868)), the southern Iberian chub (*Squalius pyrenaicus* (Günther 1868)) and the southern straight-mouth nase (*Pseudochondrostoma willkommii* (Steindachner, 1866)), although the generalised deterioration of river ecosystems limit the settlements, even within the Protected Natural Area itself, so these interactions are very occasional. Furthermore, as a result of the introduction of exotic species associated with sport fishing, the rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)) appear in some upper stretches, and the North American largemouth bass (*Micropterus salmoides* (Lacépède, 1802)), the Northern pike (*Esox lucius Linnaeus*, 1758) or the common carp (*Cyprinus carpio* Linnaeus, 1758), among others, in the middle and lower stretches. All these invasive alien species cause ecological competition, sometimes very intense, with the previously mentioned native species (Larios-López, 2017).

Without considering the introduced populations of the rainbow trout, the brown trout is the only continental fish that naturally inhabits within the boundaries of the Sierra Nevada National Park (Larios-López et al., 2015a). These trout populations, along with others that inhabit nearby mountain ranges in the southeast of the Iberian Peninsula, are the evolutionary result of those that found thermal refuge in this region after the last glacial period (Bernatchez, 2001), some 18 000 years ago. In addition, the Sierra Nevada populations possess certain particular characteristics, some of which are exclusive for their entire range (Larios-López, 2017), including (i) being the only endemic salmonid populations in the region, (ii) being peripheral populations in the southwestern geographical limit of the species, (iii) developing exclusively resident lifestyles, unlike more northerly populations in which individuals with migratory strategies - "reos" - appear (SNPRCN, 1991), (iv) possessing genetic haplotypes that are unique in the world (Almodóvar et al., 2010), (v) showing the longest and most delayed brown trout reproduction periods that have been reported in the literature (Larios-López et al., 2015b), and (v) being affected by the historical anthropogenic impact on watercourses in Mediterranean regions, intensified in recent centuries (Blondel et al., 2010). This last fact has caused an accelerated process of spatial and population regression of the brown trout in this region (Menor & Prenda, 2006, Sáez Gómez, 2010), intensifying the natural trend in the degree of threat that any species possesses as its populations approach their natural distribution edges (Hampe & Petit, 2005). In fact, at present, brown trout populations in southern Spain show a high degree of population isolation (Larios-López et al., 2015a) and the species was listed as Endangered in the Red Book of Andalusian Vertebrates (Franco Ruíz & Rodríguez de los Santos, 2001). For this reason, since 2005, the brown trout can only be fished in Andalusia in the sport modality of catch and release, a measure that, although it attempts to ease tensions with sport fishermen because it is a species with high socioeconomic value, is an incomprehensible management measure given the serious conservation status of the species in this region (Larios-López et al., 2019).

In relation to the extraordinary genetic importance of the brown trout populations in Sierra Nevada, it is imperative to emphasise that these populations include two of the six evolutionarily significant units (ESUs) observed within the Iberian Peninsula (Machordom et al., 2000) and exhibit four worldwide exclusive haplotypes (Almodóvar et al., 2010). However, a high degree of genetic introgression has been observed, which is attributed to the historical introduction of Central European specimens, primarily during the latter half of the last century. Consequently, the preservation of the integrity of these brown trout populations is imperative for the conservation of the species' genetic diversity (Almodóvar et al., 2006). Furthermore, it should be noted that all the populations of brown trout that inhabit the Andalusian Mediterranean basins are found in the Sierra Nevada and, in the case of the Guadalquivir river basin, 90% of its trout populations inhabit this mountain range. Specifically, Larios-López et al. (2015a) identified 21 populations in Sierra Nevada completely isolated in the headwaters of almost all the sub-basins that originate in the massif, from 2200 to 200 m a.s.l. (lower limits already outside the protected area). These altitudinal ranges were recently updated to 2300 - 130 m a.s.l. (*sensu* Sierra Nevada Global Change Observatory, own data). All Sierra Nevada populations have upper limits of natural origin, while their lower limits have anthropogenic origin, all of them related to water management, an over-exploited resource in the region. Therefore, the elimination of the anthropogenic impacts that currently limit these populations downstream would mean an increase in the altitudinal range of all of them and, consequently, an increase in the area inhabited by the species.

On the other hand, the age distribution of trout populations in Sierra Nevada tends to be strongly unstructured. In general, population densities tend to be low, with a greater presence of juveniles, followed by fry. The few adults are barely older than three or four years (Barquín et al., 2010, Larios-López, 2017) and the observation of specimens older than eight years is usually punctual (Zamora et al., 2015, Consejería de Sostenibilidad, Medio Ambiente y Economía Azul, 2022). Furthermore, Barquín et al. (2010) found large differences in the diet ingested by these age classes. Fry tend to feed on Ephemeroptera and Plecoptera nymphs and Diptera larvae in more than 90% of cases, while juveniles increase the amount of terrestrial invertebrates in their diet, reaching up to 50% of the intake in the case of adults. When they found that terrestrial invertebrates did not account for the majority of food drift in rivers, they deduced that adult trout either actively select these prey or find it easier to feed on them. This would indicate the importance of riparian forests as major donors of terrestrial invertebrates to the river environment and, therefore, that degradation of functional riverbanks could negatively affect the fitness and development of the adult classes.

Finally, it should be noted that populations of any species that inhabit areas located at their ecological limit (range edges) are naturally subject to strong selective processes, so that the emergence of local adaptations may be favoured (Lesica & Allendorf, 1995, Antunes et al., 2006). In the case of the populations of brown trout discussed here, not only do they inhabit a natural distribution edge of the species (they are the southernmost in Europe), but also they are resident (without anadromy), they possess the high ecological plasticity that characterises the species in terms of high genetic, ecological and morphological variability (Bernatchez et al., 1992, Pakkasmaa & Pironen, 2001, Klemetsen et al., 2003) and they are subject to the unpredictability that characterises the Mediterranean climate (stochasticity of torrential rains and periods of drought, fundamentally). According to Larios-López (2017) these four facts (distribution edge, residence, ecological plasticity and Mediterranean climate) could have acted as triggering factors in the appearance of two specific and particular ecological adaptations in these populations of brown trout. These ecological strategies refer to their reproductive period (Larios-López et al., 2015b) and their population dynamics (Larios-López et al., 2021) and would act at the population and metapopulation organisation level, respectively.

Consequently, Larios-López et al. (2015b) found that the spawning season of the brown trout in various streams of the Baetic System, including Sierra Nevada, is the longest and most delayed of all the reproductive periods reported in the literature for this species. This was established following the detection of egg-producing females from early October to late April or early May, thus giving a reproductive period of between 150 and 170 days. The question remained whether this egg production was attributable to different females reaching maturity at varying times, or whether there existed females capable of producing eggs on multiple occasions within a single reproductive period. Recent studies (Sierra Nevada Global Change Observatory, own data) have resolved some of this uncertainty by detecting females capable of producing eggs twice within the extended reproductive period described.

The other ecological response (Larios-López et al., 2021) refers to the fact that, in the southern Iberian Peninsula, the recruitment of this species (the annual density of fry) shows very significant density-independent population dynamics, as it is not influenced by the density of breeding adults (endogenous factor), but exclusively by environmental factors (exogenous factors). In particular, their recruitment is (i) negatively influenced by total winter rainfall, (ii) positively influenced by total spring rainfall and, furthermore, (iii) it is synchronised by a Moran effect (*sensu* Moran 1953). Larios-López et al. (2021) found that the metapopulation synchrony between brown trout demes in southern Spain, including those in Sierra Nevada, increases with the geographical proximity and is mainly regulated by winter precipitation and, to a lesser extent, spring and autumn temperatures. Thus, the greater the difference between the demes in terms of altitude, the River Habitat Index (IHF in Spanish; Pardo et al., 2004) value and the inhabited distance to their upper limit, the lower the synchrony of their populations and, therefore, the greater the resilience of the species as a whole to homogeneous environmental phenomena.

BIOMONITORING OF THE STREAMS OF SIERRA NEVADA

The first attempt to study aquatic macroinvertebrate communities in order to evaluate the quality, or ecological status, of Sierra Nevada stream waters was the degree thesis carried out by Lourdes García Ropero under the supervision of Professor Juan Carlos Jordana, in which they sampled the Aguas Blancas, Chico, Poqueira and Verde streams and where, in addition to an extensive physico-chemical characterisation, the results presented in terms of macroinvertebrates denoted an insufficient sampling, since in the faunal inventory (at the genus level) only 30 taxa were mentioned (Ropero García, 1984). Undoubtedly, the most complete works in this respect were those carried out on the Monachil River, studying the effects of the ski resort (Zamora-Muñoz & Alba-Tercedor, 1992), the Genil River (Madrid-Vinuesa, 1990), the Guadalfeo River (Alba-Tercedor & Jiménez-Millán, 1985, Jáimez-Cuéllar, 2004) and its basin, and the Adra River Basin (Alba-Tercedor et al., 1986). The effects of the Canales reservoir on macroinvertebrate communities (Zamora-Muñoz & Alba-Tercedor, 1996, Bello, 1997, Bello & Alba-Tercedor, 2004) and on the processes of organic matter decomposition (Casas et al., 2000) have also been studied. Moreover, within the GUADALMED project that focused on the study of the Spanish Mediterranean water courses, several streams of the Sierra Nevada were monitored along two consecutive years (Alba-Tercedor et al., 2004) and the resulting dataset was used to develop the MEDPACS (Mediterranean Prediction and Classification System), a predictive approach to the macroinvertebrate communities (Poquet Moreno, 2007, Poquet et al., 2009). A detailed analysis of the history of the biomonitoring of the Sierra Nevada watercourses can be found in Romero Martín & Alba-Tercedor (2013).

All these studies supported that in Sierra Nevada water courses, the major anthropogenic effect affecting aquatic macroinvertebrate communities is the alteration of flows and the diffuse pollution from the use of agricultural products, as well as organic sewage effluents. As a consequence of these threats, a long-term monitoring of the streams of the Sierra Nevada was urgent, as well as that of other ecosystems.

In 2007, the Spanish central government requested Andalusia to develop planning instruments to complement the Spanish Climate Change Strategy. In this sense, the Junta de Andalucía adopted a set of actions within the Andalusian Climate Change Strategy. The Sierra Nevada Biosphere Reserve was identified as a suitable place to carry out studies on Global Change in mountain environments and participated, together with 27 other Mountain Biosphere Reserves worldwide, in the International Global Change Research and Monitoring Network known as GLOCHAMORE (GLObal CHAnge in MOuntain REgions). Within this framework, the Sierra Nevada Global Change Observatory was born with the aspiration of gathering useful and relevant information on the functioning of the ecological and socio-economic systems of the Sierra Nevada, with the aim of designing management protocols that would minimise the impacts of Global Change in the mountain massif and, at the same time, could be exportable to other places.

Monitoring by the Sierra Nevada Global Change Observatory in high mountain rivers of the massif began in 2007 for the brown trout, while the collection of benthic invertebrate samples (both nymphs/larvae and adults) and the installation of water temperature dataloggers began in 2008, covering rivers on the different slopes of the Sierra Nevada (Alhorí, Alcázar, Andarax, Bayárcal, Berchules, Dílar, Genil, Lanjarón, Monachil, Poqueira Torrente and Trevélez).

After more than a decade of sampling, the set of data obtained has provided very valuable information on how the communities that inhabit the streams of the Sierra Nevada are being affected by the new climatic conditions within the Global Change framework. For instance, air temperature has increased significantly in Sierra Nevada by an average of 1.5ºC since the 1950s, with an increase in average water temperature of more than 0.5°C (Fajardo-Merlo et al., 2015, Sáinz-Bariáin et al., 2016), which means that the thermal scenario of the species has changed significantly in recent decades.

These changes in environmental conditions have favoured the rise of new species to the high mountains of Sierra Nevada, coming from lowlands or nearby mountain systems, such as *Leuctra geniculata* (Stephens, 1836) and *Leuctra cazorlana* Aubert, 1962, which were captured for the first time in 2017 in the Genil River within the limits of the massif (Fajardo-Merlo, 2021), in the case of *Leuctra cazorlana*, extending their distribution to other streams in subsequent years. This trend has been also found in other aquatic insects, such as caddisflies (Sáinz-Bariáin et al., 2016).

Also, at the community level, an increase in the richness of macroinvertebrate families was detected at high mountain levels in a comparative analysis carried out in the Monachil River (Sáinz-Bariáin et al., 2015). In this study, several taxa considered exclusive to the mid-mountains of the Monachil River in the 1980s [*Serratella ignita* (Ephemeroptera), *Perla marginata* (Plecoptera) or *Micrasema moestum* (Hagen, 1868) (Trichoptera)] were captured above 2000 m a.s.l. The same was true for several families of the orders Diptera and Coleoptera, some of which had not been captured previously in this river. In contrast, no changes in taxonomic richness were detected in the mid-high mountain localities.

The continuous monitoring of streams and rivers from the Sierra Nevada during the last years have contributed to detect particular catastrophic events and their effects on the macroinvertebrate communities. An example of this are the great floods caused by heavy rainfall, both in the Andarax River (January 2010) and in the Monachil River (March 2018), which caused drastic changes in the structure of their benthic macroinvertebrate community. Nonetheless, after these extreme events, the macroinvertebrate community in the Andarax River recovered gradually, and after only a few months it had a similar composition to the one before the flood, but the community of the Monachil river needed approximately a year and a half to recover a similar composition to the one it had previously. This could be due to the fact that the river is already clearly impacted by the ski resort, which has hindered the recovery of the area, as shown in previous studies (Zamora-Muñoz & Alba-Tercedor, 1992).

The increasing frequency of extreme climatic events may have immediate consequences for these ecosystems, and may have a greater impact on benthic fauna than constant changes in temperature and precipitation. Given that one of the hypotheses of the effects of Global Change is the increase in extreme phenomena (Jourdan et al., 2018, Coumou & Rahmstorf, 2012), long-term data provided by the temperature dataloggers installed in several streams from the Sierra Nevada, as previously mentioned, generate interesting data to be analysed. In the last decade, within the monitoring program carried out by the Sierra Nevada Global Change Observatory, these data have been used to classify the days with temperatures considered extreme, showing that these days, especially those with maximum temperatures, have increased in their frequency considerably.

Also under this monitoring program, the follow up of populations of the brown trout have been carried out. Data recorded over the last years have shown that the highest altitudinal ranges of distribution of this species in Andalusia are observed in Sierra Nevada, where the trout can be located from 2313 to 130 m a.s.l. On the other hand, the density and biomass obtained during the study period show that in most census stations there is a downward trend, and the average data for the last five years seem to indicate a certain stability in the populations, although in none of them clear signs of recovery exist that would bring the populations closer to those recorded two decades ago.

Regarding the lower limits of distribution of the monitored streams, they have suffered retractions with respect to those studied a decade earlier (described in Larios-López et al., 2015a), representing a loss of more than 30% of the habitat occupied by the brown trout. The maximum altitude currently detected and shared by numerous populations in Sierra Nevada is around 2300 m a.s.l., which could indicate the existence of an ecological limit in the study region. This altitudinal limit should be considered in future works, as its variation could reveal effects related to Climate Change, which could lead to displacements to higher stretches of the rivers. In addition, temperature increase is occurring faster in mountain areas than in other areas, so that transformations in mountain ecosystems are occurring at a faster rate. Thus, as a stressor, temperature increase is especially a component of threat to which ectothermic organisms may be particularly vulnerable.

At the sight of data obtained throughout these years of monitoring, it is important to maintain this follow up in the future, so as not to lose the uninterrupted time series of monitoring and to continue providing data that will help in the management of the streams and rivers of the Sierra Nevada.

FUTURE CHALLENGES IN THE STUDY OF THE STREAMS FROM SIERRA NEVADA

During the last 50 years, much work has been done on different aspects of the biology and ecology of animal species from the Sierra Nevada. As mentioned before, this has generated a great number of publications that, ultimately, are the basis for a correct management of streams and rivers from the massif. Nonetheless, this retrospective view of the research carried out in these systems allows us to detect some particular gaps that should be filled up in the next years. These are summarized here:

- To maintain (and promote new) long-term research strategies in the streams and rivers of Sierra Nevada, choosing reference sites for being periodically monitored. In this sense, maintaining the biomonitoring program of the Sierra Nevada Global Change Observatory is essential, even incorporating the follow up of sentinel species as early detectors of Climate Change effects, recording those key phenological events that may clearly show the response of these species to changing conditions.

- To improve the dataset on life history of species at different altitudes and under different thermal regimes. Currently, only a minor proportion of EPTC species of the total present in the massif have been studied. Also, monitoring the life cycle of some of them throughout the years could provide interesting insights on their possible adaptations to new conditions.
- To follow up changes in the distribution ranges of species in the massif, monitoring rising of the upper limits, extension of the range or its contraction, focusing on species in which their upper limit of distribution is found in Sierra Nevada. The identification and protection of those stream stretches that could behave as future thermal refuges (*sensu* Elliott, 2000) for facing Climate Change could be helpful in this respect.
- In the particular case of the brown trout, it would be desirable to establish best practices to properly develop management programs. For this species, it is essential to investigate the effects of no-kill fishing on the populations and to determine whether this practice should be maintained or whether this species should be classified as "unfishable" in Sierra Nevada. Also locating and eradicating exotic species, such as the rainbow trout, and reintroducing the native species, with haplotypes characteristic of these rivers, would be necessary to maintain the populations of this vulnerable species.

The consideration of these aspects within future research projects and programs will increase the necessary data to develop proper management strategies and to improve the current decision-making protocols, which would lead to a better conservation of life in streams and rivers from the Sierra Nevada.

DEDICATORY

We would like to dedicate this article to the memory of our colleagues and friends Antonino Sánchez Ortega, Amelia Ocaña Martín, and Carmen Zamora Muñoz, whose work notably contributed to increasing knowledge of the aquatic fauna of the Sierra Nevada.

AUTHOR CONTRIBUTIONS

All authors have contributed to the conceptualisation, preparation of the original draft, proofreading and editing of the final versión.

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