# Aquatic Animal Communities of Watercourses from Sierra Nevada

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**Abstract**

The geographical situation of Sierra Nevada and its great altitudinal gradient generate particular environmental conditions in the watercourses that flow through the massif, which determines the composition and structure of the animal community inhabiting them. Regarding invertebrates, macroinvertebrates have been the organisms more widely studied in this massif and, within them, four orders of insects: Ephemeroptera, Plecoptera, Trichoptera and Coleoptera (EPTC). In aquatic vertebrates, most studies have focused on brown trout, the most characteristic high mountain fish species of this biogeographic area. A total of 189 taxa of EPTC have been recorded up to now in the massif: 36 taxa of Ephemeroptera, 24 of Plecoptera, 41 of Trichoptera and 88 of lotic aquatic Coleoptera, showing a great diversity from the biogeographical point of view, but with only a few of them endemic to Sierra Nevada. All these animals are subject to several threats in the massif, many of them related not only to climate change, but also to human-induced pollution and alterations, such as dams, pollution from the ski resort, water diversion, or even diffuse pollution due to high stocking densities. Some species will be able to cope with changing conditions throughout particular adaptations, while others without those strategies will be more vulnerable and the first to disappear. These disturbances, together with the introduction of exotic species such as rainbow trout, also affect brown trout populations. At the community scale, few studies have accomplished the analysis of whole communities of Sierra Nevada watercourses. Most data come from the application of biological indexes to assess the ecological status of streams and rivers, though some investigations have focused on particular biocoenosis, such as those of Plecoptera or Trichoptera. All of them concluded that macroinvertebrate communities under particular climate change scenarios will probably reduce their taxa richness in comparison to the present, that generalist taxa will move upstream to higher altitude reaches, if possible, and that vulnerable taxa will reduce their distribution area. Despite all this knowledge, many gaps still remain to be fulfilled, some of them discussed in this chapter. In this sense, data coming from new research at different organization levels, from managers, and even from citizen science initiatives, will contribute to improving the knowledge and conservation measures to be developed in Sierra Nevada.

**Keywords**

Aquatic insects • Brown trout • Climate change • Macroinvertebrates • River • Stream

## 1 The Lotic Ecosystems of Sierra Nevada

The particularities of the mountain system of Sierra Nevada have an important impact on the watercourses that run along its slopes. Geologically, it is part of the Betic System and the second European mountain system in altitude, after the Alps. Due to its meridional situation within Europe, it has a representation of five out of six of the bioclimatic zones present in the Mediterranean region (from the thermo-mediterranean to the crioro-mediterranean). This massif has an East–West arrangement, with a north slope draining to the Guadalquivir

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basin (which drains into the Atlantic Ocean) and a south face draining to several of the Mediterranean river basins of southern Andalusia (which are small and steep independent basins draining into the Mediterranean Sea). Nonetheless, in the westernmost part of the mountain range, watercourses have a more radial arrangement.

The core of the mountain is siliceous, while the outermost parts are calcareous (see chapter "Geological Setting of Sierra Nevada"). Due to this geologic composition, there is more superficial water than subterranean. This has important implications, not only in the hydrological and physico-chemical characteristics of the water but also in the community of organisms that inhabits each kind of stream, as we will see below. Administratively, the water courses are managed by two administrative river basin management agents: the *Demarcación Hidrográfica del Guadalquivir* and the *Demarcación Hidrográfica de las Cuencas Mediterráneas Andaluzas* (Fig. 1).

Because of the high altitudinal gradient of the river basins that originate in Sierra Nevada, many of them with altitudes ranging from above 2500 m a.s.l. to the sea level, drastic changes occur, in some cases, in less than 50 km of the river course. This is the case of the Adra River basin, for instance, where a clear strong zonation from an epirhithron to an epipotamon has been described (Alba-Tercedor et al. 1986b). Thus, the aquatic ecosystems of Sierra Nevada have characteristics more frequently found in streams and rivers from higher latitudes. Such a great altitudinal gradient of the massif and its particular situation in the Iberian Peninsula have contributed to the special characteristics these watercourses have in a region, the Mediterranean, where other kinds of streams should be more frequent.

Sierra Nevada watercourses change their characteristics rapidly with altitude. In the core of the massif, at high altitude, where the main waterways arise, the forest is absent and the vegetation is scarce, mainly in the form of hydrophilic communities such as high-mountain grasslands and peat bogs (Salazar Mendías and Valle Tendero 2019). Disturbances in these environments are locally concentrated, mainly related to cattle, tourism, both aestival and winter (the latter due to the ski resort), and water diversion (*careos*, ditches traditionally used in high mountain streams to slow down runoff and recharge the aquifers). The Sierra Nevada streams feed on snow and precipitation, so their regime is mostly nivo-pluvial (mainly in the upper reaches, above 2000 m). On the other side, the mid and low reaches of these streams flow throughout partially disturbed riparian forests. In the siliceous part of the massif, riparian vegetation is mainly composed of alder, willow and ash forests, while in the calcareous ring of the massif, elm, poplar, and willow groves predominate (Molero Mesa et al. 1992). The fluvial regime of mid to low altitude reaches changes to pluvio-nival (Pulido 1980; Alba-Tercedor and Jiménez-Millán 1987). Overall, the effect of the snow on the streams and rivers of Sierra Nevada is more important in the westernmost part of the mountain (Castillo Martín 2001). This fact conditions the period in which the maximum discharge of water is registered on each side. Thus, western streams have discharge peaks from April to July, and minimums mainly in September and August, while eastern

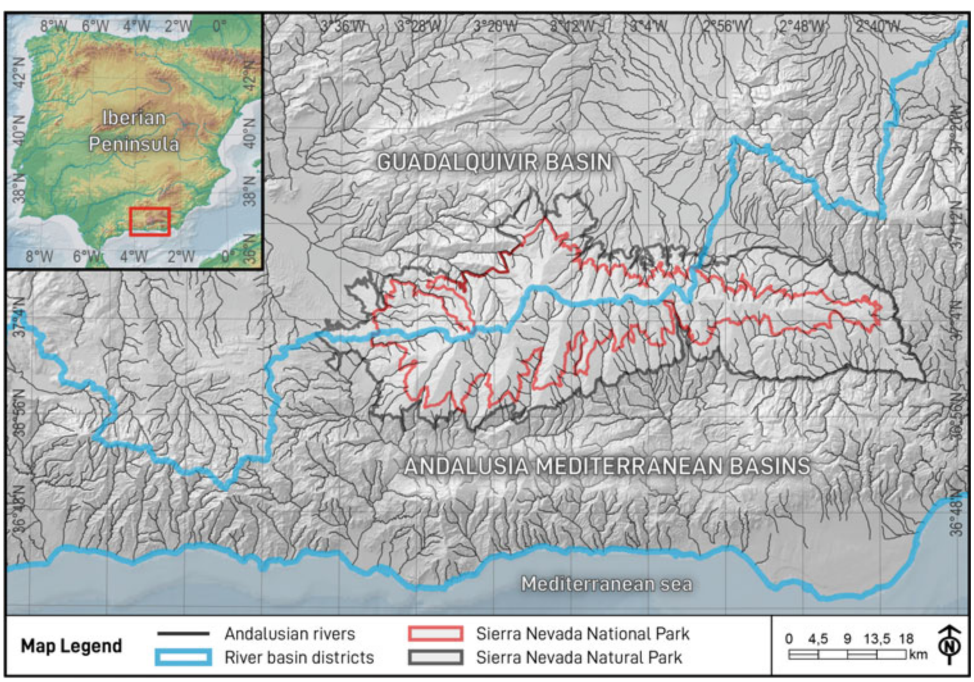


**Fig. 1** Map of Sierra Nevada showing the main watercourses that drain through it and the river basins they belong to

streams, where thaw occurs before, have peaks in February and minimums in September (Castillo Martín 2001). In general, western streams have higher discharges than eastern ones, and in the latter losses due to evapotranspiration are higher (Castillo Martín 2001).

All these environmental characteristics determine the communities of fluvial organisms found in Sierra Nevada, as well as the set of interactions that take place among the organisms that compose them. The following sections of this chapter will be devoted to them.

## 2 Who Lives There?

### 2.1 State of the Art: Current Knowledge of the Best-Studied Fluvial Macroinvertebrate Groups

Macroinvertebrates have been the focus of most studies on the invertebrate fluvial fauna of Sierra Nevada. Several M. Sc. or Ph.D. theses have been developed, totally or partially, during the past decades in the massif, which have opened different lines of research at different levels of biological organization. Within macroinvertebrates, those better studied and with a longer history of research in Sierra Nevada are mayflies (Ephemeroptera), stoneflies (Plecoptera), caddisflies (Trichoptera) and beetles (Coleoptera) (henceforth, EPTC; Fig. 2). In this sense, different authors carried out an in-deep review on the knowledge of these aquatic insect groups (in addition to other aquatic and terrestrial taxa) from Sierra Nevada (in Ruano et al. 2013). Within this review, Romero Martín and Alba-Tercedor (2013) compiled and assessed the state of knowledge (until 2010, not included) of the invertebrates from streams and rivers of Sierra Nevada after an intensive analysis of more than 300 references, including "grey literature". As pointed out by these authors, one-off records of lotic invertebrates date from the mid of the nineteenth century, but it was at the end of the 70s of the twentieth century when surveys and studies started to rise significantly. These coincide with the development of some of the M.Sc. and Ph.D. theses previously mentioned and the scientific papers derived from them, mainly on the taxonomy and biology of mayflies, stoneflies, beetles and caddisflies. Nonetheless, some interesting data come also from more general studies concerning the ecological status of water bodies and biomonitoring (e.g., Zamora-Muñoz and Alba-Tercedor 1992; Alba-Tercedor 1996; Jáimez-Cuéllar 2004; Bello and Alba-Tercedor 2005). After the intensive revision by Romero Martín and Alba-Tercedor (2013), it was concluded that despite a total of 617 species of aquatic macroinvertebrates having been listed, many taxa still remain to be recorded, because many records are based on identifications to family or genus level. Especially, there is an important lack of knowledge on the macroinvertebrate fauna at high mountain reaches (above 1700 m), and the easternmost basins are the poorest studied (the Guadiana Menor River and the Andarax River).

From then to now, some other studies have been carried out in Sierra Nevada, even expanding in some cases the study of macroinvertebrates to new fields never analyzed in these mountains before. Particularly regarding the best studied groups (i.e., EPTC), these studies have focused on different aspects of the organisms, such as behaviour (Tierno de Figueroa et al. 2009b; Tierno de Figueroa et al. 2014), life cycles and nymphal trophic ecology (López-Rodríguez et al. 2012; Sáinz-Bariáin and Zamora-Muñoz 2012; Tierno de Figueroa et al. 2019), taxonomy (Múrria et al. 2010; Olah et al. 2014; Sáinz-Bariáin and Zamora-Muñoz 2015), molecular and physiological aspects (Sanz et al. 2010, 2017; Finn et al. 2014; Boumans and Tierno de Figueroa 2016) and several other fields (Tierno de Figueroa et al. 2009a; Sáinz-Bariáin et al. 2016b; Garcia-Raventós et al. 2017; Múrria et al. 2020; Villar-Argaiz et al. 2020). Moreover, organisms collected in Sierra Nevada for other purposes have been also employed in more general studies to respond to scientific questions in a wider geographical area (Bonada et al. 2009; Hering et al. 2009; Tierno de Figueroa et al. 2010; Luzón-Ortega et al. 2013; Zhou et al. 2016; Ferreira et al. 2020), and to develop the MEDPACS (MEDiterranean Prediction And Classification System). MEDPACS is a predictive approach to the analysis of the macroinvertebrate communities of the Mediterranean watercourses (Poquet et al. 2009), a model used as a basis to predict the distributional shifts of river macroinvertebrate communities under future global change scenarios in the Spanish Mediterranean area (Alba-Tercedor et al. 2017).

### 2.2 Biodiversity of EPTC

A total of 189 species and subspecies of EPTC inhabit the fluvial environments of Sierra Nevada. For mayflies, 36 taxa have been recorded in this massif, representing one-third of the mayflies recorded in the Iberian Peninsula, though it is known that still remains new species to be described, especially Heptageniidae (Alba-Tercedor 2013). Three mayflies species present in the massif are endemic to the Iberian Peninsula, and two of them are endemic to Sierra Nevada. Regarding stoneflies, there are 24 species recorded from the 146 species cited in the Iberian Peninsula (Tierno de Figueroa et al. 2018), two of them recently found and cited in the massif (Tierno de Figueroa et al. 2013b; Fajardo Merlo 2021). Seven stoneflies species present in the massif are endemic to the Iberian Peninsula, none of them endemic to Sierra Nevada. The caddisfly diversity in Sierra Nevada is poorer than in other mountain systems probably due to the


**Fig. 2** Pictures from Sierra Nevada showing: **a** a mayfly (author: J. Alba-Tercedor); **b** two stoneflies mating (author: J. R. Fernández Cardenete); **c** a caddisfly (author: J. J. Soler); **d** an aquatic beetle (author: I. Flores Arcas); and **e** brown trout (author: E. Sofos Naveros)

harsh climate and the dominance of siliceous composition in headwater streams, which limit the distribution of caddisfly species specialized in non-siliceous ecotype. There are 41 species of caddisflies reliably cited; nine species are Iberian endemism, two of them endemic from Sierra Nevada (Sáinz-Bariáin et al. 2013). Finally, of the total number of aquatic Coleoptera species catalogued in Sierra Nevada (Sáinz-Cantero 2013), 88 of them inhabit the running waters of the massif, which constitute an important component of the macroinvertebrate communities present in this type of epicontinental aquatic environment. Of them, 11 are Iberian endemisms and one is endemic to Sierra Nevada. Most aquatic Coleoptera associated with flowing waters are typically rheophilic, among which predominates representatives of the families Hydraenidae (20 spp.), followed by Elmidae and Dytiscidae (with 10 and 8 spp, respectively). However, slightly more than 40% of these species can also be found in other freshwater environments of lentic nature (Millán et al. 2014) such as ponds, small lagoons, springs or fountains. Among this latter group of species, representatives of the families Dytiscidae (17 spp.) and Hydrophilidae (12 spp.) clearly predominate. The presence of species both in lentic and lotic environments in Sierra Nevada also occurs in Ephemeroptera (11 species) and Trichoptera (17 species).

## 2.3 Biogeographical Overview of EPTC

From a biogeographical point of view, in Fig. 3 are represented the six main elements detected in the fauna of these four aquatic insect orders in Sierra Nevada, which are based on the biogeographical categories proposed by Ribera et al. (1998) and Vigna Taglianti et al. (1999). Species with a wide geographical distribution are slightly predominant in Sierra Nevada (36.5%). These are mainly elements widely distributed in the Palaearctic region together with some representatives of Coleoptera and Ephemeroptera known from other biogeographic regions such as the Nearctic or Afrotropical. Most of them fit the Trans-Iberian chorotype defined by Ribera et al. (1998) and in general, their dispersal ability (among other biological characteristics) seems to be the explanatory factor on the basis of the available data. However, a similar proportion (31.8%), corresponds to species of European distribution according to the criteria of Vigna Taglianti et al. (1999) (Northern chorotype *sensu* Ribera et al. 1998), most of which find their geographical distribution limit in the south of the Iberian Peninsula, which clearly exceeds the elements with a Mediterranean distribution (13.8%) that are generally widespread in the southern sector of the Iberian Peninsula, despite the latitudinal location of Sierra Nevada. The orographic characteristics of the area considered, with a wide altitudinal and consequently thermal gradient, could explain this discordance in terms of the ecological preferences of the species with respect to the latter factor. The representativeness values of Iberian endemisms account for 18% of the river species catalogued, a value which is higher than that recorded for the rest of the aforementioned southern species. Of these, 41.2% are restricted to the south-eastern peninsular area (Ribera et al. 1998), including the five taxa exclusive to Sierra Nevada: *Limnebius monfortei*, *Ephemerella ikonomovi nevadensis* (formerly *Serratella spinosa nevadensis*, though this is under discussion), *Ecdyonurus* (*Ecdyonurus*) *baeticus*, *Annitella iglesiasi* and *Limnephilus obsoletus*.

## 2.4 Threats and Conservation Status of EPTC

One of the main threats for these animals is the altered environmental conditions due to climate change. These organisms will face climate change and some of them will cope with it through different strategies, avoiding or mitigating the effect of adverse conditions. The temporal evolution of precipitation in Sierra Nevada over the past 50 years has shown a general decline (Pérez-Luque et al. 2016, see chapter "Climate Variability and Trends"), the river water flow has decreased, and the average water temperature has risen by almost 2 °C (1.6) over the past 20 years. These changes have apparently had a drastic effect on the aquatic macroinvertebrate communities (Sáinz-Bariáin et al. 2016a, b). Due to this, many species of Trichoptera have been seen to move up in altitude in search of colder

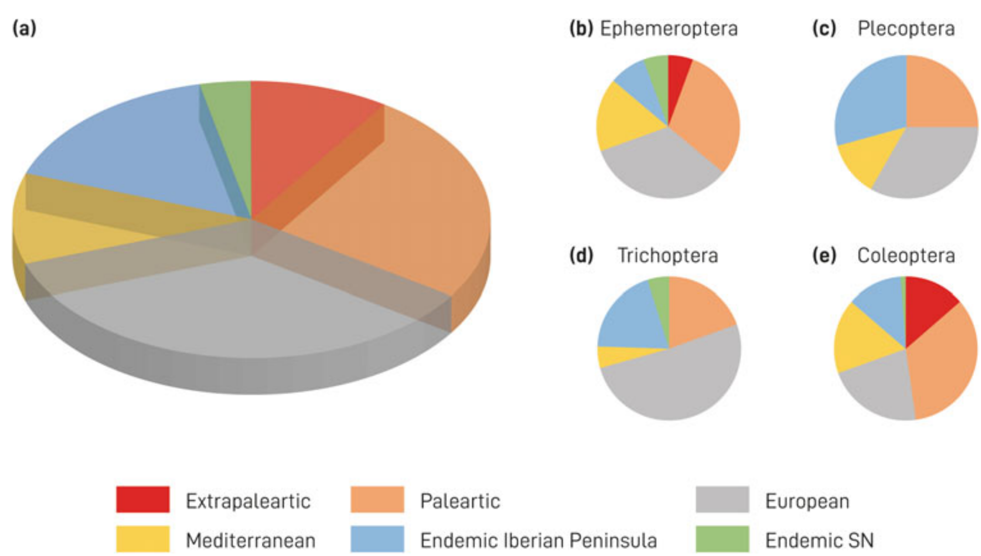


**Fig. 3** Pie charts showing the proportion of species of: **a** the four aquatic insect orders analyzed; **b** mayflies (Ephemeroptera); **c** stoneflies (Plecoptera); **d** caddisflies (Trichoptera); and **e** beetles (Coleoptera) from Sierra Nevada in each biogeographical category considered. SN: Sierra Nevada

waters. This has led to an increase in the number of species inhabiting the protected area of the Sierra Nevada National Park as a result of movements up to an altitude of 800 m in search of more suitable temperature conditions (Sáinz--Bariáin et al. 2016a, b). In relation to this, a strong change in the macroinvertebrate communities has been predicted at different global warming scenarios (Alba-Tercedor et al. 2017). This would imply that the set of interactions in each community could change, and this could have an effect on ecosystem processes such as the cycle of matter and the flux of energy. Other strategies would be those related to the alteration of the life cycle of certain species, either through the displacement of the growth period, modifications in their phenology and/or modifications of their voltinism (e.g., Sáinz-Bariáin and Zamora-Muñoz 2012). Some examples of changes of these kinds have already been related to temperature and water regime of the streams from Sierra Nevada (e.g., López-Rodríguez et al. 2008; Sáinz-Bariáin et al. 2016b), some of them triggered by the temperature regime changes induced by dams (e.g., Alba-Tercedor 1990a, b). Thus, those without strategies such as some of the ones pointed out here would be those more vulnerable in the near future (Múrria et al. 2020).

Despite the difficulties in categorizing a species as threatened, because in some cases it is not possible to determine whether what is observed is the actual status of the species or an effect of limited sampling, some Sierra Nevada mayflies species with restricted global distribution are in the red list (Verdú and Galante 2006).

Stoneflies are, due to their general high stenoecity and low dispersal capacity (favoring that many species are isolated as small populations), one of the most vulnerable and threatened animal groups in the frame of the current Global Change (Fochetti and Tierno de Figueroa 2006, 2008; Tierno de Figueroa et al. 2010). Nonetheless, only four of the approximately 3800 extant species (DeWalt et al. 2020) have been currently included in the IUCN Red data list (IUCN 2021), neither of them belonging to the European fauna despite the high percentage of species from this continent that can be considered threatened. The Red Books of Invertebrates from Spain and Andalusia include eight (Verdú and Galante 2006; Verdú et al. 2011) and four (Barea-Azcón et al. 2008) stoneflies species, respectively, neither of them present in Sierra Nevada. Nevertheless, it is remarkable the presence of relict populations of some species such as *Perlodes microcephalus*, *Perla grandis* (or *P. bipunctata*, see Tierno de Figueroa et al. 2013b), *Capnia nigra*, *Leuctra inermis* and *Taeniopteryx hubaulti* in this massif (Tierno de Figueroa et al. 2013b), whose presence in the south of the Iberian Peninsula is restricted to Sierra Nevada or, in some cases as *C. nigra*, *L. inermis* and *P. grandis/bipunctata*, also to close mountains as Sierra de Baza or Sierra de Castril. Those five species could be considered threatened at a regional scale in Andalusia or, in the case of *T. hubaulti*, in all the Iberian Peninsula (Tierno de Figueroa et al. 2013b). This threat situation is particularly true in the case of *T. hubaulti* and *P. microcephalus*, whose scarce populations have been detected in high altitude (at 2000 m or higher) in Sierra Nevada (although punctually a few nymphs have been collected at lower altitudes, what could be a consequence of the drift) and that makes those populations particularly vulnerable to the effects of climate change (see the vulnerability criteria reported in Tierno de Figueroa et al. 2010).

Caddisflies present a high taxonomic, ecological and functional diversity, being able to be found in most of the freshwater ecosystems of the world (Wiggins 2004; Morse et al. 2019). They are considered organisms sensitive to climate change mainly because: (1) they have narrow ecological niches and low dispersal capacity; (2) many species inhabit upper reaches of rivers; and (3) are cold-stenothermic species (Hering et al. 2009; Kernan et al. 2010). Around 68% of caddisfly populations are declining, more than any other group of aquatic insects (Sánchez-Bayo and Wyckhuys 2019). Of the 956 species found in the Mediterranean area, 425 are considered Mediterranean endemisms (Tierno de Figueroa et al. 2013a; Morse et al. 2019). In the Iberian Peninsula and the Balearic Islands, 368 species have been recorded, one-third endemic (González and Martínez-Menéndez 2011; Martín 2017). Only five of the approximately 16,300 extant species (Morse 2021) have been currently included in the IUCN red list (IUCN 2021), neither of them belonging to the Iberian or Mediterranean fauna. There is no caddisfly species incorporated in the Red Books of Invertebrates from Spain (Verdú and Galante 2006; Verdú et al. 2011) and, although 11 species were included in the Red Book of Invertebrates from Andalusia, 10 were catalogued in the "data deficient" category. The other one, *Annitella esparraguera*, a species present in Sierra Nevada and nearby mountains, was classified as "endangered" (Barea-Azcón et al. 2008), although this classification should be reviewed because its distribution range is wider than previously thought (Sáinz-Bariáin et al. 2013). Long-term changes have been detected in the richness and altitudinal distribution of caddisflies in Sierra Nevada, probably related to the increase in temperature and decrease in the water regime of the rivers (Sáinz-Bariáin et al. 2016a, b). It has been observed that species richness is increasing in altitude (specially at sites located between 1800 and 2000 m), as a consequence that species from middle reaches have enlarged their range of distribution towards higher elevations (*Rhyacophila meridionalis, R. nevada, Hydroptila vectis, Philopotamus montanus, Hydropsyche infernalis, Micrasema moestum, Halesus tessellatus* and *Sericostoma vittatum*), and the colonization of species with good dispersal abilities (e.g., *Stenophylax nycterobius, Allogamus mortoni*) from nearby mountain ranges (Sáinz-Bariáin et al. 2016b). Species inhabiting headwaters in high-altitude ecosystems do not have the opportunity to accommodate ecological requirements in scenarios of climate change, and could be threatened by more generalist species that are able to migrate in altitude and compete for resources. Hence, endemic species may be more vulnerable than more general species due to their lower dispersive capacity and narrow ecological requirements (Múrria et al. 2020). It has been estimated that about 50% of the Iberian species of caddisfly could be severely affected by the potential impact of climate change (Hering et al. 2009). In a study on the vulnerability to climate change for two endemic species, high-elevation and low-dispersive species of *Annitella* (*A. esparraguera* and *A. iglesiasi*) in Sierra Nevada, it was found that both species showed low genetic diversity but only *A. esparraguera* exhibit locally unique haplotypes, indicating limited gene flow. For *A. esparraguera*, modelled future habitat suitability showed 88.4% range contraction by 2050 (RCP scenario 8.5) and a displacement of 41.5% of the current potential distribution to higher elevations. Populations of *A. esparraguera* are predicted to be lost because of the reduction of optimal habitat and limited propensity for tracking future suitable conditions (Múrria et al. 2020).

Regarding the conservation status of aquatic beetles, with the exception of *Hydroporus decipiens*, which is widely distributed in the Iberian Peninsula, the rest of the endemic Coleoptera present in watercourses of Sierra Nevada have moderate to high vulnerability values according to the number of localized populations. Because of demographic data available for each of them, as well as the particular characteristics of their habitat (Sánchez-Fernández et al. 2008), a total of five endemic species present in this mountain massif are considered worthy of priority attention in terms of conservation. Among them, *Limnebius monfortei,* which is only known from its type locality in Sierra Nevada (Barranco de Las Víboras, 1500 m), is particularly noteworthy.

Apart from climate change, other important threat factors for Sierra Nevada EPTC are: (1) construction of dams, reservoirs and water diversion (*careos*), which interrupt or interfere with natural water flow, as it is the case of Canales dam in the Genil River Basin (Bello and Alba-Tercedor 2005) or the Benínar dam in the Adra River Basin (Alba-Tercedor et al. 1986a, 1986b); (2) construction of small electric plants, as in the Poqueira River; (3) punctual pollution from tourist complexes (camping sites, ski resort, etc.) or villages which alter natural water quality (Sánchez-Ortega and Tierno 1996; Zamora-Muñoz and Alba-Tercedor 1992); and (4) diffuse pollution in some high mountain streams due to, mainly, high stocking densities.

## 2.5 The Brown Trout: Threats and Conservation Status

Regarding freshwater vertebrates, fish, and particularly the brown trout, have also a relatively long history of studies. The low temperatures of the streams and rivers that flow through the Sierra Nevada massif allow the maintenance of populations of brown trout (*Salmo trutta*) as the only high mountain species characteristic of this biogeographic area (Fig. 2). In mid and low altitude reaches, outside the protected area, the increase of water temperature allows the appearance of cyprinic species such as andalusian barbel (*Luciobarbus sclateri*), southern straight-mouth nase (*Pseudochondrostoma willkommii*) and southern Iberian chub (*Squalius pyrenaicus*). However, due to the introduction of exotic species by fishermen, rainbow trout (*Oncorhynchus mykiss*) appeared inside the National Park in the mid-twentieth century and, outside it, exotic cyprinids such as north American largemouth bass (*Micropterus salmoides*), Northern pike (*Esox lucius*) or common carp (*Cyprinus carpio*), among others. At present, all these invasive alien species are naturalized (they have their "own reproductive capacity") and compete with the endemic ones with which they coexist, causing their displacement (Larios-López et al. 2015a).

After cataloguing the Andalusian populations of brown trout as threatened (Franco Ruíz and Rodríguez de los Santos 2001), the regional government started in 2005 the "Recovery Program for brown trout populations in Andalusia". In addition, this species was included in 2007 as a bioindicator of climate change within the project Global Change Observatory of Sierra Nevada (Larios-López et al. 2018). All the results obtained for this salmonid in both projects are recorded in "gray literature", but it is necessary to highlight those referring to its historical distribution (Sáez et al. 2010), the detection of high genetic diversity, with new haplotypes discovered (Almodóvar et al. 2010), the carrying capacity of rivers (Barquín et al. 2010) and estimates of ecological flow and trophic preferences (Barquín et al. 2015). Later, Larios-López et al. (2015a) identified that the upper limits of distribution of these populations are of natural origin (populations reaching the headwaters of the rivers, the highest possible altitude, or impassable waterfalls), while the lower ones are due to anthropogenic causes (impassable dams, water abstraction for irrigation and human consumption, or synergistic effects of agriculture, water diversion, water pollution and habitat fragmentation). Also, Larios-López et al. (2015b) reported the most extensive spawning period described for this species to date (from early October through late April or early May) as a result of lack of anadromy, the characteristic unpredictability of the

Mediterranean climate and the temperature range of the rivers inhabited by the species, including those of Sierra Nevada. Moreover, Larios-López et al. (2021) found that the recruitment of trout populations in the study region was a density-independent process and synchronized by means of a Moran effect. Larios-López (2017) also proposed particular adaptive management measures for these southernmost populations in Europe, probably some of the most threatened in the entire natural range of the species.

Larios-López et al. (2015a) described the main threat factors for brown trout in Sierra Nevada. In the high reaches inhabited by this species (between 1500 and 2000 m), they detected the presence of numerous specific water diversions (the aforementioned *careos*), which cause the desiccation of some stretches of the river, sometimes for more than half a kilometer away, within the Sierra Nevada Natural Park (e.g., Trevélez or Bérchules rivers). In addition, in the Monachil River, due to both the poor water quality after passing through the ski resort and the intense extraction of water that it suffers in its upper and middle section, the upper limit of this species is located at 1300 m. However, brown trout has an upper distribution limit of around 2000 m in all the other rivers of this sub-basin (Genil).

It is in the middle reaches of Sierra Nevada (700–1500 m), where most of the factors that threaten the populations of brown trout are concentrated. Uncontrolled water withdrawals greatly increase near the villages and, in summer, they cause the complete drying of some rivers. This fact limits ten populations in the lowest part of their distribution range (e.g., Bérchules, Bayárcal or Alhama de Lugros). The effect of water extraction, coupled with the decrease in quality due to the presence of numerous untreated discharges, generates synergistic effects (Gasith and Resh 1999) which lead to loss of the species in six other rivers (e.g., Monachil, Lanjarón or Dílar). In addition, poaching in these middle reaches (Larios-López et al. 2019) and the unsafe effects of the "catch and release" fishing modality (Arlinghaus et al. 2007; Cooke et al. 2013), affect the behavior, growth and reproduction of fish (Policansky 2002). Moreover, the presence of four large dams in Sierra Nevada is notable, fragmenting the populations of the Genil (Canales reservoir), Aguas Blancas (Quéntar reservoir), Guadalfeo (Rules reservoir) and Adra (Benínar reservoir) river basins. The populations that inhabit downstream of these reservoirs are significantly unstructured and disappear after a few kilometers. Associated with reservoirs, the introduction of invasive exotic fish species by fishermen is a fact (American bass, pike and common carp, among others) and, in the case of rivers, rainbow trout, that was introduced during the second half of the twentieth century in this region. Their reproductive and competitive capacity against brown trout has been proven in Sierra Nevada (Larios-López 2017). This exotic salmonid has displaced the native species of several river stretches (e.g., Genil, Alcázar), as well as in entire rivers (e.g., Arroyo del Pueblo, Ohanes). In 2009, the Regional Council for the Environment of Junta de Andalucía began an eradication program for naturalized populations of rainbow trout in Sierra Nevada with great success, by unifying this program with the introduction of populations of brown trout with genetic background typical of the region.

However, the current context of climate change anticipates extremely drastic shifts in the dynamics of these regulatory external drivers (mainly precipitation) in the study region (IPCC 2013). Longer, wetter and stormier winters are expected. These storms will also be more intense in Mediterranean systems (Ulbrich et al. 2006; Giorgi and Lionello 2008), so that the damage to fish populations will be greater since fish species are more sensitive to floods if they occur out of the natural flood regime. In this sense, Jensen and Johnsen (1999) verified the huge impact of floods reducing entire age classes of brown trout. Considering this fact, as well as that these southernmost brown trout populations of the Iberian Peninsula have population synchrony (Larios-López et al. 2021), negative environmental disturbances would have the capacity to endanger their resilience. This phenomenon would be even greater in Sierra Nevada, both due to the devastating predicted effects of climate change and the high degree of isolation that the species presents on this distribution edge.

## 3 Changes at the Population and Community Level

### 3.1 Key Ecological Factors Acting on Macroinvertebrate Communities

Most macroinvertebrate community studies have been carried out at the family level due to the complexity of reaching a lower taxonomic resolution with many aquatic stages of several groups (Romero Martín and Alba-Tercedor 2013). Furthermore, most of this information comes from analyses conducted to determine the ecological status of the water bodies through biotic indexes such as the IBMWP, which only needs identification of macroinvertebrates at the family level (Alba-Tercedor and Sánchez-Ortega 1988; Alba-Tercedor 1996, 2000; Alba-Tercedor et al. 2004). Despite the lack of more specific information on these approaches, they can provide a good general overview of the status of the macroinvertebrate communities of streams and rivers from Sierra Nevada, mainly when analyzed together with the major physicochemical parameters of the water.

Key abiotic features of the environment that usually drive the abundance and distribution of macroinvertebrates are those related to current, substrate, temperature, and sometimes water chemistry variables such as alkalinity and dissolved oxygen (Allan et al. 2021). In the context of climate change, water temperature and flow are probably two of the most important, as they will likely be affected in future scenarios due to global warming and changes in the precipitation patterns (IPCC 2013; Alba-Tercedor et al. 2017). Both temperature and spatial variation in hydraulic parameters have been shown to affect the local distribution and abundance of stream macroinvertebrates (Vannote and Sweeney 1980; Allan et al. 2021). This may be especially noteworthy in high mountain streams such as those of Sierra Nevada, where increased temperatures and decreased river water flow over the last 40 years have been already detected (Sáinz-Bariáin et al. 2016b).

Few investigations have accomplished the study of whole communities of Sierra Nevada watercourses, and those that have done it have focused mainly on the application of biotic indexes to assess the ecological status of streams and rivers, as mentioned before. For instance, Zamora-Muñoz and Alba-Tercedor (1996) surveyed the macroinvertebrate communities of several streams of the Genil River basin, measured water physicochemical parameters and assessed the ecological status of the waters using biotic indices, as the BMWP' (posteriorly called IBMWP). The studies carried out in the Monachil River revealed that sewages from the ski resort located at the head of the river drastically reduced the diversity of macroinvertebrates, collecting only taxa highly tolerant to organic pollution (Zamora-Muñoz and Alba-Tercedor 1992; Zamora-Muñoz et al. 1993). In the Genil River Basin, nutrient content and water hardness were the main factors influencing macroinvertebrate distribution. Most of the sites in the study area were polluted, and consequently the most frequently collected taxa were tolerant species. Moreover, the worsening of the quality downstream was accompanied by a substitution of species, sometimes within the same genus, from less to more pollution tolerant (Zamora-Muñoz and Alba-Tercedor 1996). On the other hand, Alba-Tercedor et al. (1986a, b) and Jáimez-Cuéllar (2004) surveyed the ecological status of two basins, Adra and Guadalfeo river basins, using the IBMWP index and, additionally, carried out an assessment of the β-diversity of the communities in both rivers, as well as a study on the relationship between the biocoenosis of the main aquatic insect orders and the physicochemical characteristics of the studied reaches. These authors found that β-diversity decreased downstream (with one occasional exception in the Adra River) due to progressive deterioration of streams and rivers. In a more recent study performed as part of a scientific project in four basins of Sierra Nevada (Dílar, Genil, Trevélez and Poqueira Rivers) during two seasons (autumn and spring), some unpublished preliminary data showed that, though the overall ecological status and α-diversity were high in most reaches (Fig. 4), those situated under particular sources of disturbances suffered a drastic reduction in these parameters (see, for instance, the T3 sampling station in Fig. 4, situated downstream of the Trevélez village). In this study, communities were affected by anthropogenic impacts, but some studies have also projected the effect on macroinvertebrate communities of climate change related impacts, such as temperature and flow reduction. This is the case of a research using the MEDPACS predictive approach simulating three different climatic scenarios of water temperature increase and water flow reduction, in which Alba-Tercedor et al. (2017) concluded that the lotic macroinvertebrate communities of the Iberian Peninsula will probably reduce their taxa richness in comparison to present. Moreover, generalist taxa were predicted to move upstream to lower temperature reaches and vulnerable taxa would reduce their distribution area. A similar conclusion was reached previously by Tierno de Figueroa et al. (2010) and by Sáinz-Bariáin et al. (2016b) studying stoneflies and caddisflies biocoenosis, respectively.

### 3.2 Key Ecological Factors Acting on the Macroinvertebrate Populations

At the population level, again water temperature and flow are two of the most important extrinsic factors modulating the biology of macroinvertebrates in general, and of aquatic insects in particular (Sweeney 1984; Allan et al. 2021). To study this, some species of Ephemeroptera, Plecoptera and Trichoptera have been monitored in the massif, several of them during a whole year. In particular, López-Rodríguez et al. (2008) determined that differences in temperature regime (measured as day-degrees accumulated by the species) affected population dynamics of several species of mayflies, either due to changes in the growth rate (as occurred with *Serratella ignita* and *Ephemerella ikonomovi nevadensis*, reported as *S. spinosa nevadensis*), or due to changes in voltinism (as in *Baetis muticus*, reported as *Alainites muticus*, and *Baetis alpinus*). These authors also concluded that the effect of temperature on the studied stonefly species was less drastic, just advancing, delaying or displacing the life cycle some months.

Other important factors that act on the populations of several aquatic insects are those related to pollution and habitat degradation (Fig. 5). Though Sierra Nevada is a protected area, some anthropogenic impacts can still be found in the mountains, the most important of them related to the ski resort within the Natural Park. In this sense, is the Monachil River the fluvial axis in which the effect of the pollution generated in the ski resort of Sierra Nevada becomes more apparent (Zamora-Muñoz and Alba-Tercedor 1992). Alba-Tercedor et al. (1991) analyzed the impact of this area on the mayfly and stonefly biocoenoses of several reaches in the Monachil River and they found that the

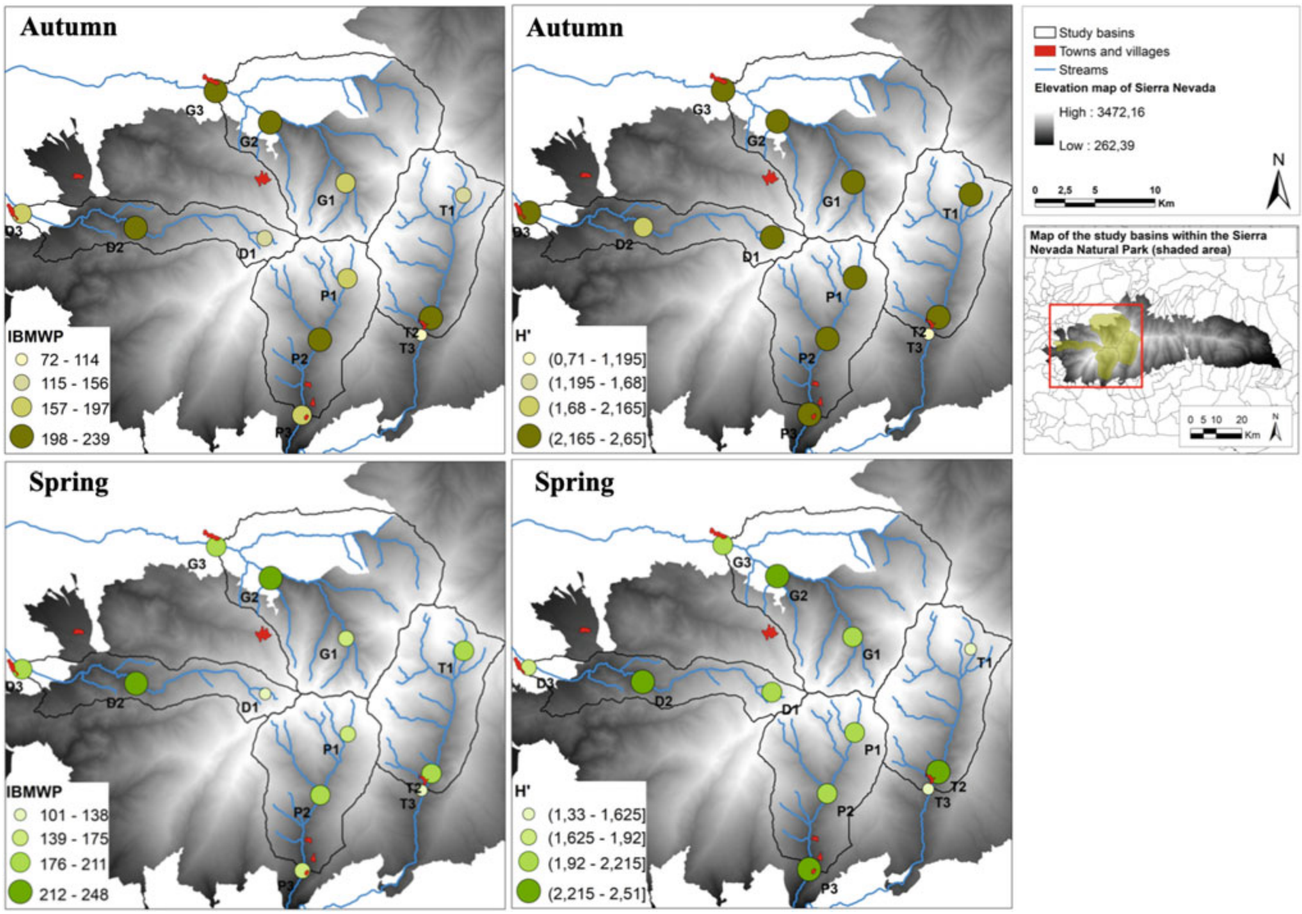


**Fig. 4** Map showing reaches from the Dílar (D), Genil (G), Trevélez (T), and Poqueira (P) Rivers in which both IBMWP and Shannon–Wiener diversity (H´) were assessed (figure courtesy of Ander Congil Ross). Variations in both indexes occur within watercourses and between seasons (spring and autumn) due to changes in environmental conditions, and in some cases due to inefficient wastewater purification (e.g., T3)

populations of most species declined with altitude and in relation to pollution of lower altitude sites. Afterward, Zamora-Muñoz et al. (1993) analyzed the effect of several physicochemical parameters on the distribution of mayflies and stoneflies in the same river. These authors found that the distribution of ten of the 15 species of mayflies and two of the 12 species of stoneflies studied by them was significantly influenced by one of the environmental parameters assessed. These parameters were, in order of importance, water temperature, content of calcium, nitrates, dissolved oxygen, pH and phosphates, some of them related to organic pollution, and the most affected species by the organic pollution were *Baetis rhodani*, *Isoperla nevada* and *Leuctra inermis*.

Regarding habitat degradation, one of the main and more obvious impacts on stream connectivity are dams (Allan et al. 2021). Depending on their size, they can isolate stream reaches almost completely, so they have an important effect on the structure of communities downstream (e.g., Bello 1997; Bello and Alba-Tercedor 2005) and even on ecosystem-scale processes such as leaf decomposition (Casas et al. 2000).

## 3.3 Key Ecological Factors Acting on the Brown Trout Populations

The effect of ecological parameters on aquatic vertebrates, particularly brown trout, has also been accomplished in streams and rivers of Sierra Nevada. With this goal, Larios-López et al. (2021) investigated the drivers of their population dynamics in the region between 2006 and 2014. They proved that recruitment is not regulated by density-dependent mechanisms and that there is not even a positive effect on the reproductive stock. Specifically, rainfall

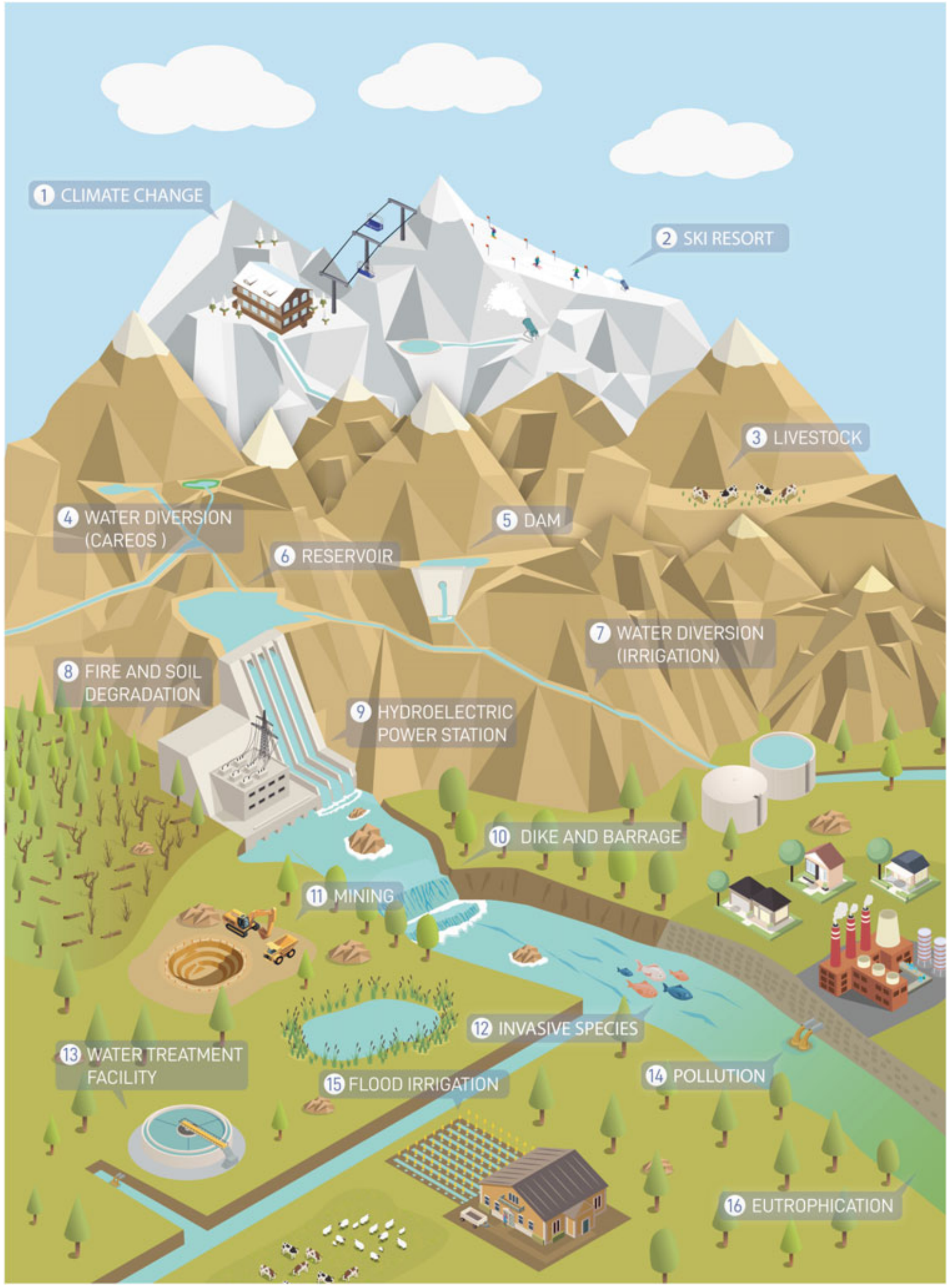


**Fig. 5** Schematic diagram of the main threats to aquatic fauna of Sierra Nevada. The key risks to aquatic fauna include climate change (1), water regulation and extraction processes (2, 4, 7, 9, 15), interception activities including reservoirs and dikes (5, 6, 10), land use degradation (8), impacts of mining, industry and water pollution (11, 14), invasive species (12), and eutrophication due to livestock and inefficient sewage water purification (3, 13, 16)

is the only external driver that explains the recruitment dynamics in this area (negatively affected by winter rainfall and positively affected by spring rainfall). Moreover, juvenile density is determined by the density of young-of-the-year during the previous year, while there is no significant effect of the density of juveniles during the previous year on the density of adults in a given year. All these results could be expected in populations inhabiting their rear edges of distribution (*sensu* Hampe and Petit 2005), where the extreme conditions prevent populations reaching an equilibrium density. This is the case of brown trout in Sierra Nevada, where densities are below the carrying capacity and relatively free of intraspecific competition, unlike the central European core areas where the density-dependent factors are involved in regulating populations. Moreover, Larios-López et al. (2021) showed that brown trout populations in this European southern region are synchronized as a result of a Moran effect (as previously mentioned) directed mainly by winter precipitation and conditioned by the habitat similarity between populations (highlighting altitude, distance to the upper limit, geographic distance and result of IHF index; see Pardo et al. 2002). Therefore, the greater the differences in these factors of habitat similarity, the lower the synchrony of the populations and, therefore, the greater the resilience of the species as a whole against homogeneous environmental phenomena.

### 3.4 Connecting the Elemental and the Ecosystem Level

Recently, the study of the elemental and biochemical content of benthic macroinvertebrates has become a focus of research in Sierra Nevada. This field known as biological stoichiometry examines how the balance of energy and different elements influence living systems (Sterner and Elser 2002). The analysis of elemental carbon (C), nitrogen (N) and phosphorus (P) composition of 436 specimens collected from four high mountain streams of Sierra Nevada revealed that macroinvertebrate C:N:P stoichiometry differs among taxonomic groups but not among functional feeding groups, and is largely due to changes in P content (Villar-Argaiz et al. 2020). Although numerous studies have documented similar results at the species level (e.g., Liess and Hillebrand 2005), very few studies have examined ontogenetic variation within a given taxon and still a consensus is lacking in the literature regarding ontogenetic patterns in P content. Thus, while most studies have shown that for a given taxa small individuals have invariably higher P content than large individuals (Back and King 2013), Villar-Argaiz et al. (2020) reported over threefold increases in the P content from small to large *Dinocras cephalotes* (Plecoptera). The findings of positive relationships between P content and body mass in Sierra Nevada are undocumented in the literature and, most intriguingly, they were exclusively found for hemimetabolous insects. Because elemental composition reflects body demands, the study of stoichiometry can therefore be used to understand how organisms respond to changes in resource quality and quantity facing current global change.

Knowledge of how P content varies across ontogeny is essential because P plays a key role in the growth rate, a most crucial life trait driving the evolutionary fitness of animals (Sterner and Elser 2002). The observation that rapidly growing organisms have a high P content compared to slower growing organisms gave rise to the “growth rate hypothesis”, which states that elevated growth rates demand large amounts of P linked to the RNA needed to sustain rapid protein synthesis (Elser et al. 2003). The success of the growth-rate hypothesis in improving our understanding of the mechanistic variation between P content, C:P stoichiometry and growth rate has paved the road to the extrapolation of biological stoichiometry to the domain of evolutionary ecology. Collectively, these studies suggest that variations in C:N:P ratios in macroinvertebrates reflect underlying allocations to major molecules such as RNA versus DNA. This idea, initially tested in crustacean zooplankton (Hessen et al. 2008), and referred as to the “growth rate-genome size-nutrient limitation” hypothesis, claims that P limitation in chronically limited environments could be behind the evolutionary tradeoff between P allocation to RNA for rapid growth at the expense of low DNA content and reduced genome size (Hessen et al. 2009). In a study on the nucleic acid content of 639 specimens of benthic macroinvertebrates in Sierra Nevada, Villar-Argaiz et al. (2021) extended this hypothesis to insects with different metamorphosis modes, and found that differences in allocation between RNA and DNA may reflect fundamental evolutionary tradeoff between rapid growth rate and high RNA content in holometabolans at the expense of diminished genome sizes relative to hemimetabolans (Villar-Argaiz et al. 2021). By connecting elements, macromolecules, and key life-history traits such as growth rate and organisms evolutionary fitness, these studies contribute to bridge the gap between different layers of biological organization from genes to ecosystems.

## 4 Concluding Remarks: What Else Can Be Done?

Sierra Nevada streams and rivers are subject to a wide range of pressures and impacts (a schematic summary of them can be found in Fig. 5), and there is still much to be studied about the macroinvertebrates of the massif watercourses and the effect of these pressures on them. Romero Martín and Alba-Tercedor (2013) underlined that many groups are still very poorly known, and that detailed and systematic studies of large areas above 2000 m are needed. In fact, though in the last decade there have been intensive surveys of, for instance, particular groups of aquatic insects in the massif, new species are still being recorded for the first time in the mountains (e.g., *Leuctra geniculata*, *L. cazorlana*, *Stenophylax nycterobius*, *Allogamus mortoni, Adicella reducta, Agapetus fuscipes, Glossosoma boltoni, Meladema coriacea*, *Limnebius* (*Limnebius*) *bacchus*, *L.* (*Limnebius*) *ignarus*, *Hydrochus grandicollis*). This could be a mix of changes in the distribution ranges of these species and of an intensification of the samplings during the past years. In this sense, the Global Change Observatory of Sierra Nevada, with the support of the Environment and Water Agency of Andalusia, is performing a monitoring program that is generating interesting data (both faunistic and in relation with the ecological status of several water stream reaches) and that should be maintained in the future to reach a long-term record of macroinvertebrate and fish communities. This kind of data will allow us to analyze the effect of climate change on these communities and to propose the most realistic mitigation measures.

Some important gaps in the assessment of lotic macroinvertebrate communities from Sierra Nevada are related to the analysis of the role of these organisms in the food webs they belong to. Studies of these aspects still lack in Sierra Nevada, and are fundamental to actually understand the flux of energy and matter in these particular environments. Inferences from other sites or from different taxonomic levels have proved not to work properly (e.g., Tierno de Figueroa et al. 2019), so specific analyses of gut contents or other techniques (such as stable isotopes) should be applied to these organisms in each studied reach.

In the case of the brown trout, the generation of climate models for the Sierra Nevada massif under different climate change scenarios would be an interesting tool. In this way, it would be possible to predict its effect on river courses and, therefore, foresee changes in the current distribution of the species, as in studies carried out in other peninsular regions (Almodóvar et al. 2012; Ayllón et al. 2017; Clavero et al. 2017; Santiago et al. 2017). This research would allow the detection of specific river stretches in Sierra Nevada that could behave, in the future, as thermal shelters (Elliott 2000) against climate change (Daigle et al. 2014). Furthermore, it would be very interesting to expand the investigations initiated by Larios-López et al. (2021), with the intention of verifying the effect of precipitation and summer temperature on the population dynamics of the species.

Finally, the implication of the whole society is essential for maintaining the ecological status of watercourses from Sierra Nevada and, mainly, for avoiding their deterioration. In this sense, the "citizen science" initiatives are an important tool to reach these objectives. The collaboration among society, scientists and managers is the only possible way to face future Global Change scenarios and to properly handle and carry out the mitigation measures needed to stop the inertia of deterioration of these wonderful and interesting environments.

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