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Habitat use and species associations of Odonata in Sierra Nevada (Spain)

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ABSTRACT

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This study examines the factors influencing the composition of Odonata communities in Sierra Nevada, a distinctive biogeographic region in the southeastern Iberian Peninsula. Odonates are valuable indicators of freshwater health, facing threats from both climate change and human-induced habitat alterations. Effective conservation strategies rely on thorough ecological assessments analysing the relationship between species and their environment. Sierra Nevada's diverse habitats and climatic gradients provide a unique setting for this research. We conducted quarterly sampling of larvae over three years (2012-2014) at 216 stations covering lotic (rivers, streams) and lentic (ponds, pools) habitats. Physicochemical variables and habitat characteristics were recorded. Generalised Linear Latent Variable Models (GLLVM) were used to analyse species interactions and the influence of environmental variables on community composition. The research revealed a diverse odonate fauna of 29 species (34.5% Zygoptera; 65.5% Anisoptera). Species richness and community composition varied significantly with habitat and altitude, ranging from 1 to 11 species per location (mean = 3.18 ± 2.45). Some species were widespread, while others were found in specific habitat or altitudinal preferences. Abundance analysis highlighted two dominant species: *Cordulegaster boltonii* in lotic and *Libellula depressa* in lentic habitats. GLLVM analysis identified distinct clusters of odonate species and their key environmental drivers. In lotic habitats, distinct associations included a *C. boltonii* dominance zone in headwaters and a basic rheophilic association at lower altitudes. In lentic habitats, a basic lentic association characterised by *Pyrrhosoma nymphula*, *L. depressa*, *Sympetrum meridionale* and *Sympetrum striolatum* prevailed in high-altitude ponds. This study underscores the importance of considering the variability in larval ecology of damselflies and dragonflies for effective conservation planning. Our findings advance the understanding of odonate ecology in Mediterranean high-altitude ecosystems, providing crucial knowledge for developing informed conservation strategies amidst environmental change.

KEY WORDS: Odonata, Zygoptera, Anisoptera, larvae, dragonflies, damselflies, Sierra Nevada, Spain, habitat use, species associations, species richness, environmental variables, Generalised Linear Latent Variable Models (GLLVM).

RESUMEN

Uso del hábitat y asociaciones de especies de Odonata en Sierra Nevada (España).

Este estudio examina los factores que influyen en la composición de las comunidades de Odonata en Sierra Nevada, España, una región clave en el sureste de la Península Ibérica. Los odonatos son valiosos indicadores de la salud del agua dulce, enfrentando amenazas del cambio climático y alteraciones del hábitat. La conservación efectiva requiere evaluaciones ecológicas detalladas que analicen la relación entre especies y su entorno. La diversidad de hábitats y gradientes climáticos de Sierra Nevada ofrecen un escenario único. Se realizaron muestreos trimestrales durante tres años (2012-2014) en 216 estaciones en hábitats lóticos (ríos, arroyos) y lénticos (estanques, charcas). Se registraron parámetros fisicoquímicos y características del hábitat. Se usaron Modelos Lineales Generalizados de Variables Latentes (GLLVM) para analizar las interacciones entre especies y la influencia de las variables ambientales en la composición de la comunidad. La investigación reveló una fauna diversa de 29 especies de odonatos (34.5% Zygoptera; 65.5% Anisoptera). La riqueza de especies y la composición de la comunidad variaron con el hábitat y la altitud (1 a 11 especies por lugar; media = 3.18 ± 2.45). Algunas especies fueron generalistas, mientras otras mostraron preferencias específicas. El análisis de abundancia destacó como especies dominantes a Cordulegaster boltonii *en hábitats lóticos y* Libellula depressa *en lénticos. El análisis GLLVM identificó agrupaciones de especies de odonatos y las variables ambientales clave que las definen. En hábitats lóticos, se distinguieron una Zona de Dominancia de* C. boltonii *en cabeceras y una Asociación Reófila Básica a menor altitud. En hábitats lénticos, una Asociación Léntica Básica, dominada por* Pyrrhosoma nymphula, L. depressa, Sympetrum meridionale*, y* Sympetrum striolatum, *prevaleció en estanques de elevada altitud. Este estudio subraya la importancia de considerar las distintas ecologías larvales de zigópteros y anisópteros para la planificación de la conservación. Los hallazgos mejoran la comprensión de la ecología de los odonatos en ecosistemas mediterráneos de alta montaña, proporcionando conocimiento crucial para desarrollar estrategias de conservación informadas frente al cambio ambiental.*

PALABRAS CLAVE: *Odonata, Zygoptera, Anisoptera, larvas, libélulas, Sierra Nevada, España, uso del hábitat, asociaciones, riqueza, variables ambientales, Modelos Lineales Generalizados de Variables Latentes (GLLVM).*

INTRODUCTION

Understanding the factors influencing species presence is crucial for effective conservation and management (Le Gall et al., 2018). Studies of local species assemblages are essential for increasing our knowledge of species distribution and habitat conservation (Leandro et al., 2017). Species assemblages are shaped by environmental variables at various landscape scales, and local habitat heterogeneity contributes to regional species pools. Aquatic environments are among the most vulnerable ecosystems and play a vital role in maintaining global aquatic biodiversity and providing crucial ecosystem services (Wang et al., 2021, Muruganandam et al., 2023). Climate change, particularly around the Mediterranean basin, is reducing water availability through decreased summer precipitation, increased evapotranspiration, and altered snowmelt (IPCC Climate Change, 2021). This leads to unstable flow regimes and drying in aquatic ecosystems, especially affecting species reliant on permanent running water (Riservato et al., 2009). Human activities exacerbate climatic events, threatening aquatic species distributions (Sayer et al., 2025). The increasing pressures of climate change and human activities on freshwater ecosystems are not only affecting individual organisms but also fundamentally changing the connections between them (Harabiš & Hronková, 2020). For the effective conservation and management of freshwater habitats, ecological assessments and biomonitoring programmes are essential (Stoddard et al., 2008, Vadas et al., 2022). These assessments must include the collection of detailed data on aquatic communities in both natural and impacted habitats, as well as an analysis of their relationships with environmental variables (Hering et al., 2006, Vitecek et al., 2021). Crucially, such studies are necessary to inform conservation strategies.

Odonata also play a central role in the conservation of freshwater habitats (Clausnitzer et al., 2009, Šigutová, et al., 2023). For this reason, the distribution of species richness within Europe for odonates of lentic and lotic habitats and of species endemic to Europe has been revisited recently (Boudot & Kalkman, 2015, Kalkman et al., 2018, 2022). Odonates, which have an obligate dependence on aquatic habitats for larval ontogeny, are increasingly threatened by climate-induced alterations in water body permanence. Although certain species have evolved adaptive mechanisms such as desiccation-resistant ova or accelerated larval development (De Block & Stoks, 2005, Maynou et al., 2025), a substantial proportion exhibits protracted larval developmental periods (Corbet et al., 2006), rendering them particularly susceptible to fluctuations in water availability (Stoks & Córdoba-Aguilar, 2012). Fluctuations in water permanence exert significant selective pressures on Anisoptera assemblages of larvae, influencing species persistence at the community level. Anisopteran larvae are frequently employed as bioindicators in the rapid assessment of freshwater ecological integrity due to their extended aquatic phase and sensitivity to various ecosystem attributes (Chovanec & Waringer, 2001, Golfieri et al., 2016, Dolný et al., 2021, Gómez-Tolosa et al., 2022, Olsen et al., 2022b). In general, species diversity exhibits a positive correlation with adequate prey availability (McPeek, 2008), and macrophyte presence is crucial for both foraging success and predator defence of larvae (Brito et al., 2021, Vilenica et al., 2022). Nevertheless, larval survival is subject to a multitude of environmental constraints (Sayer et al., 2025). Predation represents a substantial selective pressure, particularly for zygopteran larvae, which have demonstrated reduced growth rates in lentic habitats with established fish populations (McPeek, 2008). Additionally, anthropogenic pollutants and diminished water transparency can exert deleterious effects on larval fitness, foraging efficiency, and predator avoidance capabilities (Perron et al., 2021, Vilenica et al., 2021). Ontogenetic challenges during the larval stage of odonates must be carefully considered in conservation efforts, which often separate Zygoptera and Anisoptera due to their distinct adult ecologies (Peeters et al., 2025). These inter-subordinal disparities, encompassing aspects such as body size, behavioural patterns, and dispersal capacity, translate into distinct habitat requirements, notably as zygopterans exhibit weaker flight capabilities and endophytic oviposition strategies in contrast to the more versatile flight and diverse oviposition behaviours observed in anisopterans (Corbet, 2004). A key example is the divergent oviposition strategies between Zygoptera and Anisoptera, reflecting distinct evolutionary responses to ecological niches. Zygoptera employ specialized, high-investment endophytic laying (e.g., *Lestes macrostigma*), inserting eggs into living aquatic plants while often coupled in tandem (Lambret, 2024). This protects eggs from predation but exposes them to hypoxia and thermal stress. Conversely, Anisoptera, such as those in the family Libellulidae or species like *Anax imperator*, utilize a lower-investment exophytic strategy, dropping eggs directly into water or surface substrates, which allows for faster colonization of unstable habitats but increases vulnerability to predation and abiotic factors.

The divergent strategies in early odonate development invalidate a uniform conservation approach, thereby necessitating species-specific conservation plans (Corbet, 1980, Matushkina, 2011, Laaß & Hoff, 2015, Lambret et al., 2015, Harabiš et al., 2019). Consequently, conservation efforts must address the unique habitat requirements and ecological pressures faced by the egg and larval stages of each suborder, carefully considering larval-specific vulnerabilities alongside adult ecological requirements. The larval microhabitat preferences similarly show a marked contrast that transcends flow velocity. Larvae of *Coenagrion mercuriale* are typically found in slow-flowing, vegetated waters, exhibiting a high tolerance for turbidity and a specific requirement for high salinity and moderate temperature. Conversely, *Cordulegaster boltonii* larvae inhabit faster-flowing stream sections, where they face distinct challenges related to high flow velocity and substrate stability (Ferreras-Romero & Corbet, 1999).

Analysing habitat usage, understood as the affinity or preference of each species for different types of aquatic habitats and environments, is fundamental for the conservation of the species found therein, particularly dragonflies, in the current context of climate change (Hassall & Thompson, 2008, Clausnitzer et al., 2009, Ott, 2010, Hassall, 2015). On the other hand, climate change is modifying the distribution and composition of freshwater insect communities in mid and high mountains, of which Sierra Nevada is a significant case (Arroyo et al., 2022, López-Rodríguez et al., 2022). Undoubtedly, land management in the vicinity of continental aquatic ecosystems is vitally important for their conservation, due to their condition as receptors of alterations caused by human activity (Wildermuth, 2010). This fact strongly modifies the degree of maturity, heterogeneity and consolidation of aquatic ecosystems and the dragonfly species that can be established. This circumstance is especially relevant in the surroundings of populations and in agricultural areas located on the slopes of river channels. Knowledge of dragonfly and damselfly biology and ecology in Spain has significantly increased since the 1980s, leading to a reasonably good understanding of the order Odonata. Pioneering studies from researchers like Ferreras-Romero (1989a), García-Avilés et al. (1995), Pérez-Bote et al. (2006), and Torralba Burrial et al. (2007) have been instrumental in this progress.

Despite this general advancement, large geographical areas within the Iberian Peninsula still lack specific, detailed studies on odonates. The Sierra Nevada mountains serve as a prime example of this research gap (Cano Villegas et al., 2013, Conesa Garcia, 2013, Ferreras-Romero & Tierno de Figueroa, 2013, Romero Martín, 2019). This is particularly notable given that the first records for the region date back to the early 20th century (Navás, 1902, 1911). Species defining lentic communities exhibited a greater ability to track changes in their climatic niche, likely due to enhanced dispersal capability of the adult stage, which is essential given the ephemeral nature of their breeding sites (Hof et al., 2006, 2012) and definition of the larva ecological niche (Olsen et al., 2022a, Sentis et al., 2022). Lentic species, with their greater dispersal ability, are likely to exhibit enhanced resilience to environmental change. This contrast in resilience compared to lotic species likely stems from variations in how environmental stressors, such as climate change (O'Neill et al., 2024), eutrophication, and other forms of habitat degradation, affect these distinct habitat types and their associated fauna. This is due to their greater dispersal ability, which allows them to avoid uninhabitable conditions through mechanisms such as long-distance migration or a diapause state (Corbet, 2004, Heiser & Schmitt, 2010, Pinkert et al., 2018). The contrasting spatial and temporal characteristics of lotic and lentic freshwater systems impose different ecological constraints on their inhabitants. The ephemeral and discontinuous nature of most lentic water bodies may increase the importance of dispersal for lentic species, whereas species inhabiting more stable lotic habitats are suggested to exhibit lower dispersal (Grewe et al., 2013). However, high dispersal ability, while not always correlating with larger geographical ranges, can facilitate the maintenance of populations across extensive areas (Letsch et al., 2016).

With the aim of contributing to environmental quality assessments, this study sampled larvae to determine Odonata assemblages and analysed their relationships with environmental variables separately in lotic and lentic habitats of Sierra Nevada (Southern Spain). The core objective of this study was to characterise the species richness and composition of Odonata larval species assemblages in the Sierra Nevada's lotic and lentic aquatic habitats. The research aimed to determine the influence of environmental variables on their distribution and identify recurrent species associations using GLLVM. A comparison of community structures between lotic and lentic systems was performed to assess differences in habitat use. Ultimately, this research seeks to provide baseline ecological data for conservation planning in high-altitude Mediterranean ecosystems.

MATERIALS AND METHODS

Study Area

The Sierra Nevada massif is located in Southeastern Iberian Peninsula (Almería and Granada provinces; 37º 5’N, -3º 9’W) (Fig. 1). Spanning 200 000 hectares, it is the highest mountain range in the Iberian Peninsula, with peaks reaching up to 3479 m (Mulhacén peak) and an altitudinal range from 280 m a.s.l. This area exhibits significant climatic and altitudinal gradients, encompassing five of the six bioclimatic zones of the Mediterranean region and supporting diverse high-altitude ecosystems. This exceptional biodiversity, including a high number of endemic species, led to its designation as a Biosphere Reserve (1986), a Natural Park (1989), and a National Park (1999). The geology of the massif, characterised by a complex superposition of tectonic units, directly influences the water chemistry of its aquatic systems. The siliceous

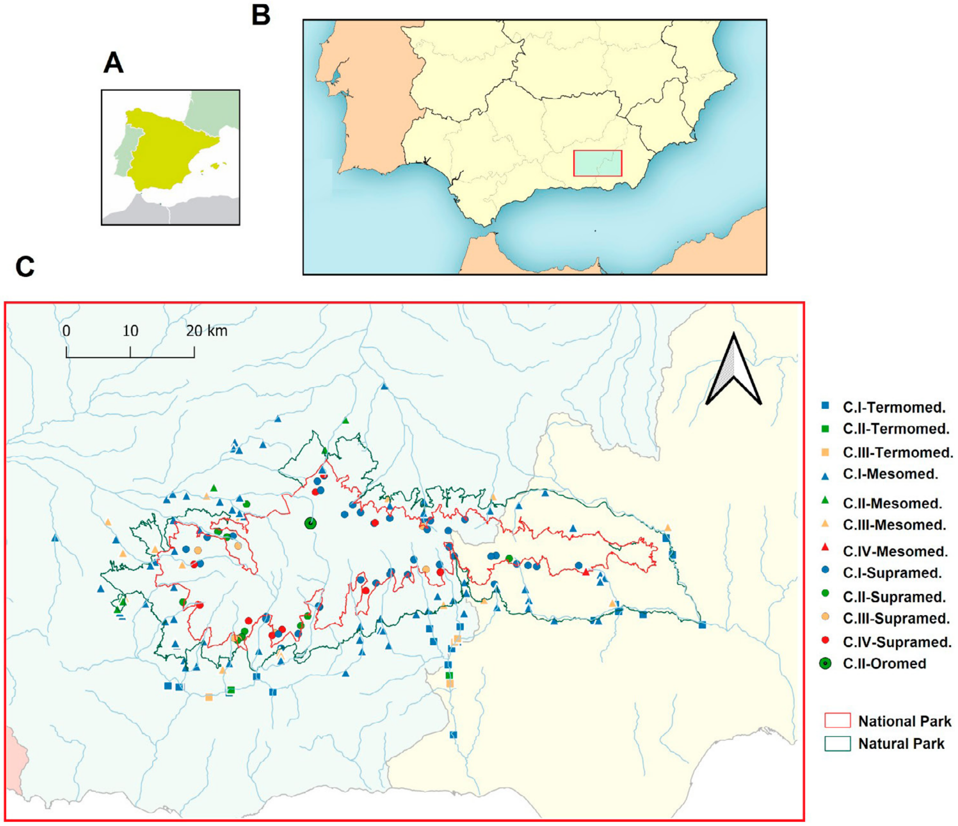

Figure 1. Location of sampling points within Sierra Nevada National and Natural Park, southeastern Iberian Peninsula. The map shows the geographic extent of the park and the specific locations where samples were collected for this study. These sampling points are represented by different colors and shapes depending on the class and bioclimatic belt. *Localización de los puntos de muestreo dentro del Parque Nacional y Natural de Sierra Nevada, sureste de la Península Ibérica. El mapa muestra la extensión geográfica del parque y las ubicaciones específicas donde se recogieron muestras para este estudio. Estos puntos de muestreo están representados por diferentes colores y formas según la clase y el piso bioclimático.*

rocks of the basal Nevado-Filábride Complex generate low-mineralisation and slightly acidic waters. In contrast, the overlying Alpujárride Complex, rich in limestones and dolomites, increases the carbonate concentration, resulting in harder waters at mid and low altitudes (Sanz de Galdeano, 2023). This lithological contrast creates distinct habitat conditions across the altitudinal gradient.

Sampling

In this study, a "sampling site" was defined as a volume or mass of water capable of supporting aquatic insect larvae, both natural and artificial, lotic or lentic, permanent or temporary. A total of 216 sites were sampled quarterly during the years 2012-2014 (Romero Martín, 2019). The study involved sampling within five hydrological catchments, namely, from East to West: Andarax, Adra, Fardes (a tributary of Guadiana Menor), Guadalfeo and Genil. Larvae were collected using a kick net with a pentagonal section of 25 cm per side, a 1.5 m handle, and a 50 cm deep net made of Nytex mesh with a 1 mm mesh size. A similar sampling effort was applied to all habitats considered (Bried et al., 2012). For the identification and study of the captured specimens, general taxonomic keys (Carchini, 1983, Askew, 2004, Doucet, 2016, Conesa-García, 2021) were used, as well as specific scientific articles and papers focused on the genera and species of dragonflies under study (Butler, 1993, Seidenbush & Heidemann, 2006, Brochard & van der Ploeg, 2013, Conesa & Cano-Villegas, 2013, Conesa & Bernal, 2017).

Habitat Classification

The Sierra Nevada massif is characterised by a pronounced altitudinal gradient that supports five distinct bioclimatic belts (Rivas-Martínez, 1980, Marfil et al., 2017). These belts, defined primarily by temperature and precipitation indices, exhibit a progressive decrease in mean temperature with increasing elevation. It is important to note that the altitudinal limits of these belts vary slightly between the northern and southern faces of the mountain range due to differences in sun exposure and associated microclimatic conditions. The five belts were: Thermomediterranean (<600 m a.s.l.); Mesomediterranean (600–1400 m a.s.l.); Supramediterranean (1400–2000 m a.s.l.); Oromediterranean (2000–2800 m a.s.l.); and Crioromediterranean (>2800 m a.s.l.). We established 216 sampling sites across a broad elevational gradient, ranging from 240 m a.s.l. to 2639 m a.s.l., to analyse habitat use and odonate species assemblages. Sampling covered all five bioclimatic belts, from the Thermomediterranean to the Crioromediterranean. Sites yielding odonata larvae were distributed from the Thermomediterranean up to the Oromediterranean (with Lavaderos de la Reina being the single highest positive site). With each of these altitude belts, the sites were further categorised into four distinct habitat types (García-Avilés et al., 1995):

- Class I. Lotic waters: all lotic water types, including rivers, streams, irrigation ditches, and canals (143 sites).
- Class II. Natural lentic waters: natural or naturalised lentic water bodies (25 sites).
- Class III. Artificial lentic environments: ponds, reservoirs and dams (37 sites).
- Class IV. Unique aquatic microhabitats: unusual aquatic microhabitats for dragonflies (ephemeral pools, springs, vertical seepages, drainage ditches, and roadside trenches), where larvae develop directly in soil saturated with a thin film of water a few millimetres thick (11 sites).

The distribution of sampling points across these habitat and elevational categories is provided in Table 1. This two-tiered classification approach allowed us to assess habitat use and species associations at both a broad, elevational scale and a fine-grained, habitat-specific level. Thirteen environmental variables were measured in each site. A Crison MM 40 multi-parameter water quality analyser and a Crison OXI 45 were used to measure physicochemical variables: water temperature [WT, °C], air temperature [AT, °C], pH, electrical conductivity [EC, µS/cm], total suspended solids [TDS, mg/L] and dissolved oxygen [DO, mg/L]). Site characteristics, considering major environmental stressors for the study area, encompassed both the origin and ecological status of the locations. These assessments were comprehensive, taking into account habitat class (categorised as I–IV), lotic or lentic typology, riparian vegetation characteristics, and the bank erosion status. They also included an analysis of the degree of waste presence and wastewater contamination levels, alongside a general envi-

Table 1. Distribution of sampling locations by bioclimatic belt (thermomediterranean to supramediterranean) and class (I-IV). *Distribución de los lugares de muestreo por piso bioclimático (termomediterráneo a supramediterráneo) y clase (I-IV).*

	Bioclimatic belt			
Habitat class	**Thermomed.**	**Mesomed.**	**Supramed.**	**Total**
I	20	83	40	143
II	3	6	16*	25
III	3	22	12	37
IV	1	1	9	11

Note: * Includes one oromediterranean site.

Table 2. List of recorded species with associated taxonomic and sampling data. The table includes the family, scientific name, and acronym used in Figures 3-9 for each species. Sampling data presented are the total number of individuals captured, abundance, number of locations where present, and percentage of presence. *Lista de especies registradas con datos taxonómicos y de muestreo asociados. La tabla incluye la familia, el nombre científico y el acrónimo utilizado en las Figuras 3-9 para cada especie. Los datos de muestreo presentados son el número total de individuos capturados, la abundancia, el número de lugares donde está presente y el porcentaje de presencia.*

Family	Species	Acronim.	N. ind.	Abund.	N. sites	Presence (%)
Calopterygidae	*Calopteryx haemorrhoidalis* (Vander Linden, 1825)	Calhae	1557	11.12	60	28.30
	Calopteryx virgo (Linnaeus, 1758).	Calvir	342	2.44	8	3.77
	Calopteryx xanthostoma (Charpentier, 1825).	Calxab	26	0.19	4	1.89
Lestidae	*Chalcolestes viridis* (Vander Linden, 1825).	Chavir	120	0.86	10	4.72
	Lestes barbarus (Fabricius, 1798).	Lesbar	33	0.24	1	0.47
	Sympecma fusca (Vander Linden, 1820).	Symfus	35	0.25	3	1.42
Coenagrionidae	*Coenagrion mercuriale* (Charpentier, 1840).	Coemer	18	0.13	3	1.42
	Enallagma cyathigerum (Charpentier, 1840).	Enacya	4	0.03	1	0.47
	Ischnura graellsii (Rambur, 1842)	Iscgra	110	0.79	14	6.60
	Pyrrhosoma nymphula (Sulzer, 1776).	Pyrnym	892	6.37	47	22.17
Aeshnidae	*Aeshna cyanea* (Müller, 1764).	Aescya	7	0.05	2	0.94
	Aeshna mixta Latreille, 1805.	Aesmix	39	0.28	6	2.83
	Anax imperator Leach, 1815.	Anaimp	536	3.83	43	20.28
	Boyeria irene (Fonscolombe, 1838).	Boyire	656	4.69	48	22.64
Gomphidae	*Onychogomphus uncatus* (Charpentier, 1840).	Onyunc	489	3.49	26	12.26
Cordulegastridae	*Cordulegaster boltonii* (Donovan, 1807).	Corbol	4501	32.15	150	70.75
Libellulidae	*Crocothemis erythraea* (Brullé, 1832).	Croery	144	1.03	23	10.85
	Libellula depressa Linnaeus, 1758.	Libdep	1908	13.63	51	24.06
	Orthetrum brunneum (Fonscolombe, 1837).	Ortbru	370	2.64	44	20.75
	Orthetrum cancellatum (Linnaeus, 1758).	Ortcan	14	0.10	3	1.42
	Orthetrum chrysostigma (Burmeister, 1839).	Ortchr	476	3.40	28	13.21
	Orthetrum coerulescens (Fabricius, 1798).	Ortcae	436	3.11	34	16.04
	Sympetrum fonscolombii (Selys, 1840).	Symfon	25	0.18	3	1.42
	Sympetrum meridionale (Selys, 1841).	Symmer	312	2.23	17	8.02
	Sympetrum sinaiticum Dumont, 1977.	Symsin	49	0.35	8	3.77
	Sympetrum striolatum (Charpentier, 1840).	Symstr	875	6.25	39	18.40
	Trithemis annulata (Palisot de Beauvois,1807).	Triann	7	0.05	5	2.36
	Trithemis kirbyi Selys, 1891.	Trikir	19	0.14	3	1.42
	Zygonyx torridus (Kirby, 1889).	Zygtor	1	0.01	1	0.47

ronmental quality assessment. All these environmental variables were quantified during every site visit. While most variables were quantified using a simple binary scale (1 or 2), the more complex parameters—specifically the degree of waste presence and wastewater contamination levels, and environmental quality assessment—utilised a more detailed five-step ordinal scale. This scale ranged from 1 (Near-Natural/Minimal Impact) to 5 (Severely Degraded/Extreme Impact), aligning with the five-class system (High, Good, Moderate, Poor, Bad) commonly employed in habitat and ecological status assessments for aquatic environments. This quantification strategy is an adaptation of the River Quality Index (RQI) (González del Tánago & García de Jalón, 2011), and the Rapid assessment of habitat condition (ECELS index) (Sala et al., 2004, Quintana et al., 2015) that considers wetland hydromorphological aspects, the presence of human pressures in the surroundings and the conservation status of the wetland vegetation.

Data analyses

All statistical analyses were performed using R 4.4.2 software (R Core Team, 2024). To assess the interactions of species within and among communities, we employed the multivariate approach Generalised Linear Latent Variable Models (GLLVM) using the gllvm package (Niku et al., 2019). GLLVM is an extension of the general linear model, adapted for multivariate data through a factor analytic approach. This approach incorporates latent variables, representing water and habitat quality for each site, along with species-specific factor loadings to quantify correlations among species. GLLVM therefore allows for the identification of taxa-specific interactions while simultaneously accounting for the influence of environmental parameters characterised as latent variables. The use of GLLVM presents several significant advantages over ordination techniques (e.g., Non-metric Multidimensional Scaling, NMDS) for the analysis of multivariate ecological or biological data. Notably, this method facilitates the testing of hypotheses concerning the relationships between species and environmental variables, and enables the quantification of the strength and direction of these relationships with associated standard errors and *p*-values within a unified framework accommodating binary data (Harrow-Lyle & Kirkwood, 2022). Furthermore, the latent variables derived in GLLVM can be directly related to species' responses and environmental gradients, thereby fostering a more ecologically meaningful understanding of the underlying factors structuring the data. The application of GLLVM to our data allows uncovering the latent structure of the community composition, revealing the relationships between species and environmental variables and enabling the exploration of species co-occurrence patterns. The coefplot() function was used to visualise the estimated coefficients of predictor variables and their confidence intervals, facilitating the examination of environmental variable effects on species. Poisson, zero-inflated Poisson, and negative binomial distributions were fit to the data. Information criterion (AIC, AICc, BIC), Dunn–Smyth residual plots, and normal quantile–quantile plots with 95% confidence intervals were used to assess the goodness of fit for odonate communities distributions (Niku et al., 2019). All analysis were performed both for the complete dataset and separately for lotic and lentic stations. In each case, the analysis was conducted considering 1 to 3 latent variables. Comparative analyses were conducted using models that either included or excluded environmental variables as random effects, with the aim of determining the contribution of these factors to the observed variation. The resulting estimations for correlation patterns across frequently occurring species were plotted using the corrplot and gclus packages (Wei et al., 2017, Hurley & Hurley, 2019). The statistical significance of the correlations displayed in the corrplot was evaluated using a bootstrapping approach with 1000 replicates. This involved generating bootstrap replicates, and the resulting *p*-values, stored in the p_mat output of the corrplot function, were used to derive bootstrap support values for each correlation. The graphics were generated using ggplot2 package. QGIS 3.34.14 was employed to map the sampling locations within the hydrographic basin and delineate the boundaries of the Sierra Nevada Natural Park and National Park.

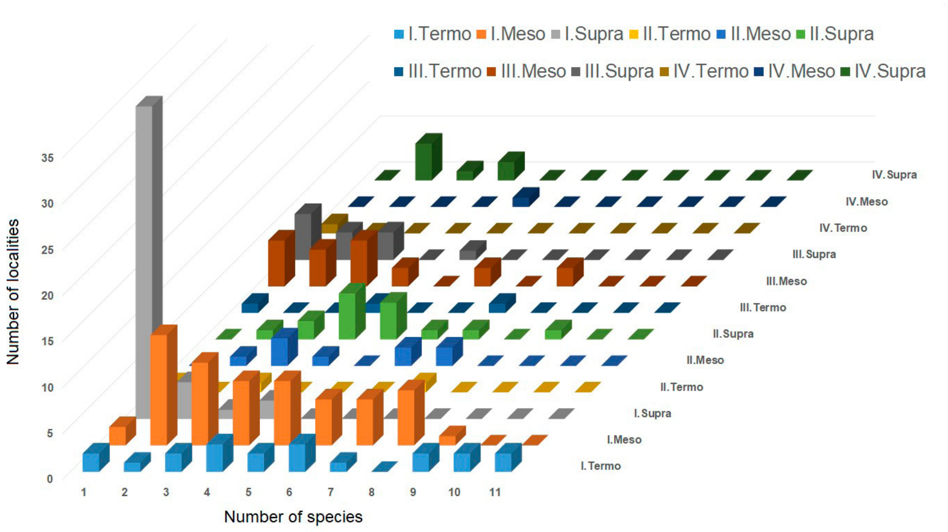

Figure 2. Frequency distribution of sampling locations based on the number of species detected per location, categorised by class and bioclimatic belt. *Distribución de frecuencia de los lugares de muestreo en función del número de especies detectadas por lugar, categorizadas por clase y piso bioclimático.*

RESULTS

A total of 29 dragonfly species were recorded during the survey (Table 2). Of these, 10 belonged to the suborder Zygoptera (34.5% of the total) and 19 were identified as Anisoptera (65.5%). The number of species found at each location ranged from 1 to 11, with a mean of 3.18 ± 2.45 species per site (Fig. 2). Regarding larval abundance, a total of 14 001 larvae were captured. The number of larvae per site ranged from 1 to 593, with an average of 64.82. Due to their scarce occurrence in Sierra Nevada, four species were excluded from the community analysis. (i.e., *Lestes barbarus*, *Enallagma cyathigerum*, *Aeshna cyanea* and *Zygonyx torridus*). Data analysis was conducted considering the entire set of selected species (n = 25) and by separating them into two distinct habitat types: Lotic (sampling points belonging to class I) versus lentic (those included in classes II-IV). The analysis of lotic sites included 19 species, while the lentic analysis included 20 species (all except *Calopteryx xanthostoma*, *Calopteryx virgo*, *Boyeria irene* and *Onychogomphus uncatus*). As depicted in figure 2, the most frequent number of species was observed in class I sampling locations within the supramediterranean belt, characterized by the exclusive presence of *Cordulegaster boltonii*, occasionally with *Libellula depressa*, *Calopteryx haemorrhoidalis*, *Orthetrum brunneum*, and/or *Orthetrum coerulescens*.

Altitudinal distribution range

As shown in figure 3, the studied species exhibited a wide range of altitudinal distributions. Some species tolerate conditions across a broad altitudinal range being present along practically the entire sampled gradient (e.g., *Sympetrum striolatum*, *Sympetrum meridionale*, *Pyrrhosoma nymphula*, or *L. depressa*), while others are confined to narrow elevational bands in the warm stations (*C. xanthostoma*, *Trithemis annulata*, *Trithemis kirbyi*, *Sympetrum fonscolombii*, and *Sympetrum sinaiticum*). Ten species reach the maximum altitudinal value, reaching or exceeding 2000 m a.s.l., while 11 species have been detected below 1000 m a.s.l., beneath the limit of the mesomediterranean zone. The species relative abundances were classified into three distinct dominance categories (Table 2). The first category was characterised by the absolute dominance of *C. boltonii* (32.14%), followed by *L. depressa* (13.63%) and *C. haemorrhoidalis* (11.12%). A second category included species with dominance values ranging

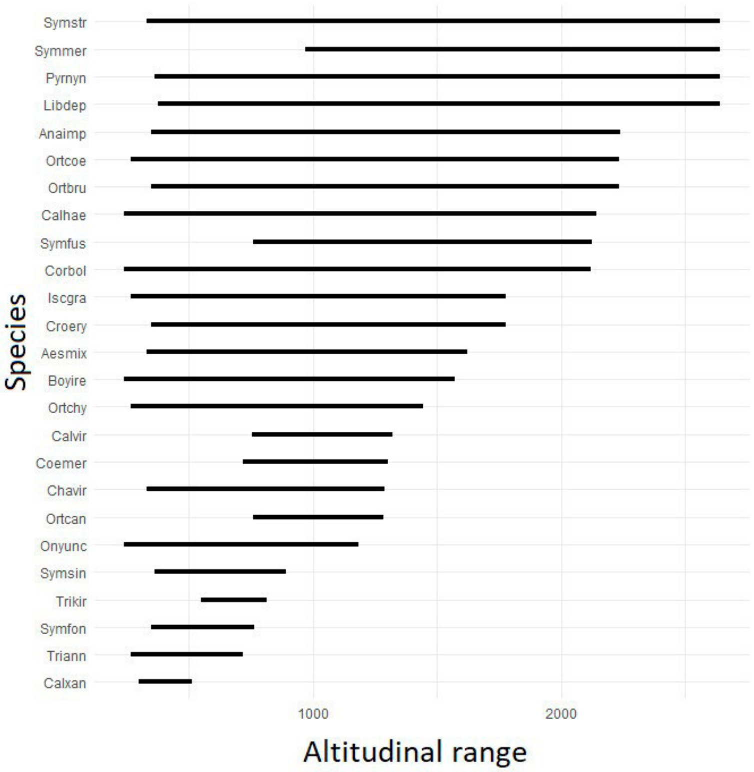

Figure 3. Altitudinal ranges of species recorded. Acronyms as in Table 2. *Rangos altitudinales de las especies registradas. Acrónimos como en la Tabla 2.*

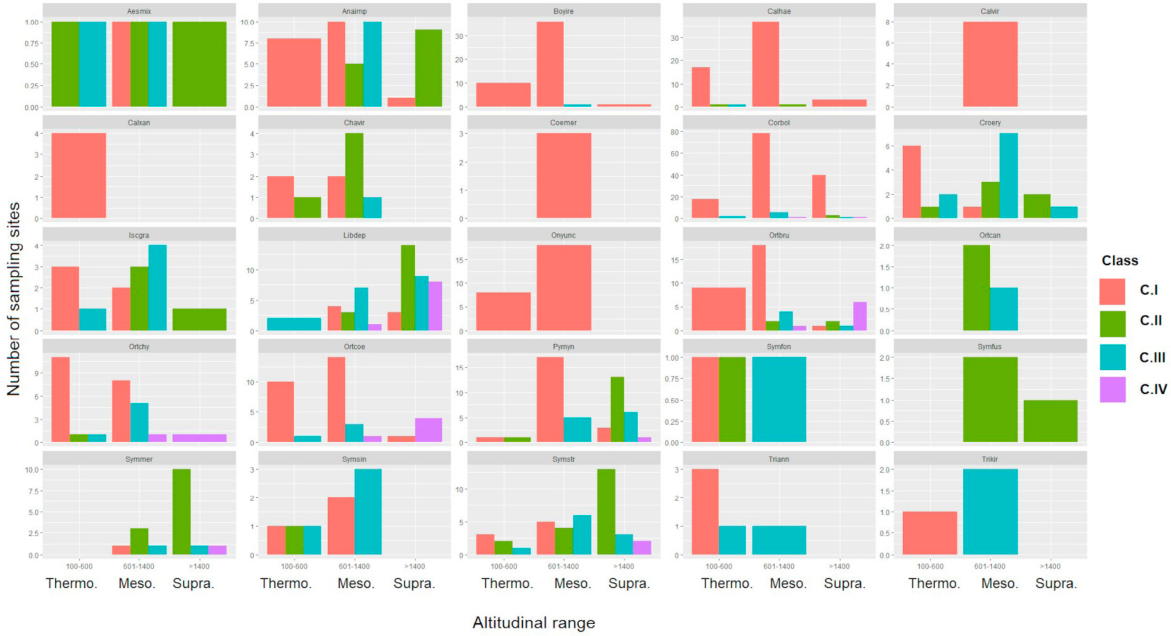

Figure 4. Relationship between the number of individuals present and the bioclimatic belt and class of the sampling point. Acronyms as in Table 2. *Relación entre el número de individuos presentes y el piso bioclimático y la clase del punto de muestreo.*

from 2% to 7%. This group comprised *C. virgo*, *P. nymphula*, *S. striolatum*, *B. irene*, *A. imperator*, *O. uncatus*, and three species of *Orthetrum* (*O. chrysostigma*, *O. coerulescens* and *O. brunneum*). The third category, which contained the largest number of species, showed dominance values of 1% or less. This low-abundance group included *Chalcolestes viridis*, *L. barbarus*, *Sympecma fusca*, *C. mercuriale*, *E. cyathigerum*, *A. cyanea*, *Aeshna mixta*, *Crocothemis erythraea*, *T. annulata*, *T. kirbyi* and *Z. torridus*. Although the families Platycnemidae and Corduliidae have been previously cited in the Iberian Peninsula, no species from these families were recorded in the present study. Based on their high abundance and consistent presence throughout the study, *C. boltonii* and *L. depressa* were the dominant species in lotic and lentic habitats, respectively. For each species, figure 4 illustrates the relationship between the number of individuals present and the bioclimatic belt and class of the sampling point.

Analysis of the species assemblage

A GLLVM was developed using a negative binomial distribution (NB-GLLVM), as it provided the best fit for the data. This model was used to identify two unmeasured latent variables that represented underlying ecological gradients driving species interactions. The final model was then selected to reveal how these latent variables were influenced by four key environmental drivers: water temperature, altitude, O_2, and habitat quality. Based on the obtained model, figure 5A illustrates the species correlation values, which reveal the presence of two distinct clusters. The first cluster is a tightly-knit group composed of *C. boltonii*, *B. irene*, C. virgo, *C. haemorrhoidalis*, and *O. uncatus*, along with *C. mercuriale* and *C. xanthostoma*. A strong association among *L. depressa*, *A. imperator*, *C. erythraea*, *O. brunneum*, and two *Sympetrum* (*S. meridionale* and *S. striolatum*) is a particularly

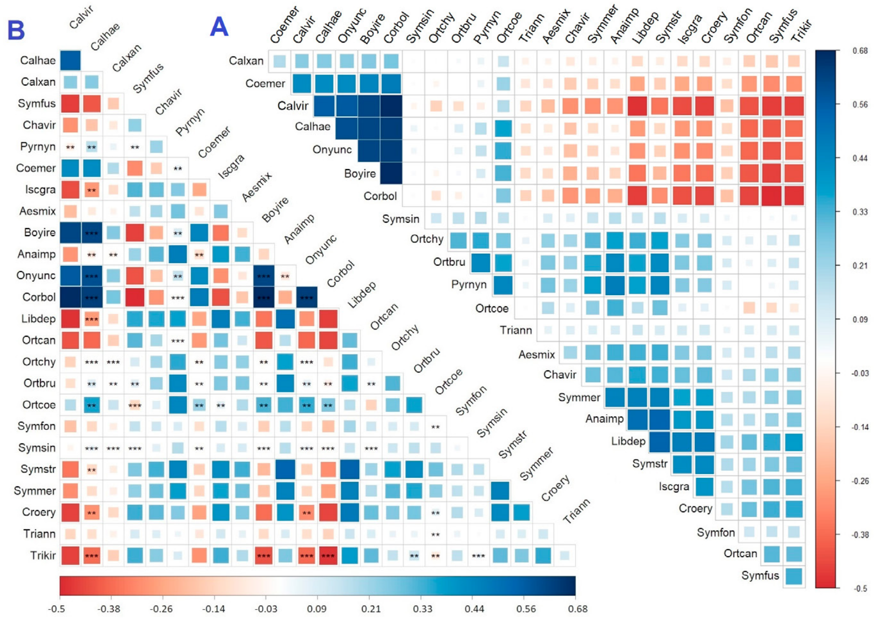

Figure 5. Correlation values obtained from GLLVM models applied to the total sampling data. A. Correlation values derived from a GLLVM negative binomial model applied to the species assemblage (N=25) and 216 sampling locations. Species are ordered using the hclust option from the corrplot package. The model was generated using four latent environmental parameters (water temperature, altitude, O_2, environment quality) and considering only two latent variables. B. Unordered correlation matrix. Significant correlations are indicated by asterisks based on bootstrap *p*-values (****p* < 0.001, ***p* < 0.01). Acronyms as in Table 2. V*alores de correlación derivados de un modelo GLLVM binomial negativo aplicado al conjunto de especies (N=25) y 216 lugares de muestreo. Las especies están ordenadas utilizando la opción hclust del paquete corrplot. El modelo se generó utilizan-do cuatro parámetros ambientales latentes (temperatura del agua, altitud,* O_2*, calidad del entorno) y considerando solo dos variables latentes. B. Matriz de correlación sin ordenar para el conjunto de datos donde las correlaciones significativas se indican con asteriscos basados en los valores* p *del bootstrap (**** p *< 0.001, *** p *< 0.01). Acrónimos como en la Tabla 2.*

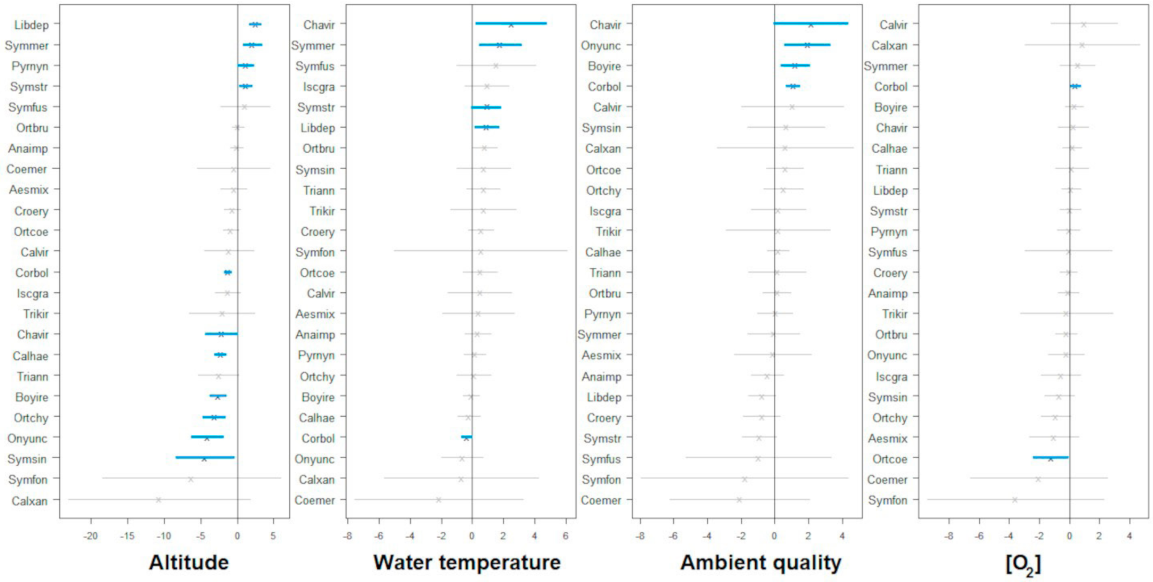

Figure 6. Estimated coefficients and 95% confidence intervals for environmental predictors from the Negative Binomial GLLVM. This plot illustrates the nature of the effects of environmental variables on species. Point estimates for coefficients are shown as ticks, with lines representing their 95% confidence intervals. Intervals coloured in grey indicate those containing zero, while blue lines denote intervals that do not contain zero (indicating a statistically significant effect at the 95% confidence level). Note that the x-axis for the coefficient plot of the third environmental variable is truncated due to a very wide confidence interval for one of the coefficients. Acronyms as in Table 2. *Coeficientes estimados e intervalos de confianza del 95% para los predictores ambientales del GLLVM binomial negativo. Este gráfico ilustra la naturaleza de los efectos de las variables ambientales sobre las especies. Las estimaciones puntuales de los coeficientes se muestran como marcas, con líneas que representan sus intervalos de confianza del 95%. Los intervalos coloreados en gris indican aquellos que contienen cero, mientras que las líneas azules denotan intervalos que no contienen cero (lo que indica un efecto estadísticamente significativo con un nivel de confianza del 95%). Nótese que el eje x para el gráfico de coeficientes de la tercera variable ambiental está truncado debido a un intervalo de confianza muy amplio para uno de los coeficientes. Acrónimos como en la Tabla 2.*

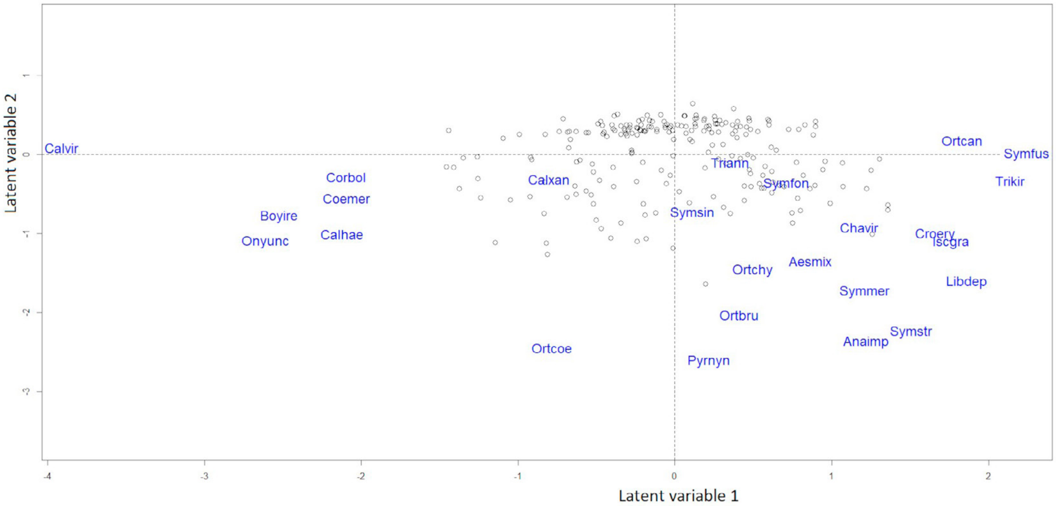

Figure 7. Ordination plot derived from the Negative Binomial GLLVM with two latent variables. The axes show the two latent variables developed by the model, visualising the inferred ecological structure of the species assemblage (N=25). Acronyms as in Table 2. *Gráfico de ordenación derivado del GLLVM binomial negativo con dos variables latentes. Los ejes muestran las dos variables latentes desarrolladas por el modelo, visualizando la estructura ecológica inferida del conjunto de especies (N=25). Acrónimos como en la Tabla 2.*

notable feature of the second cluster. Uniquely, the conditions that define the structure of both clusters appear to be suitable for *O. coerulescens*, positioning it outside of either group. Figure 5B displays the unordered correlation matrix with superimposed bootstrap support values. The estimated coefficients of predictor variables and their corresponding confidence intervals are presented in figure 6. Point estimates (ticks) and 95% confidence intervals (lines) for the NB-GLLVM coefficients are illustrated, where grey (black) denotes intervals that do (not) include zero. The ordination plot (Fig. 7), derived from a Negative Binomial Generalised Linear Latent Variable Model (NB-GLLVM) with two latent variables, effectively visualises the inferred ecological structure of the 25-species community. The position of each species on the two-dimensional axes reflects its association with the underlying latent variables, thereby revealing potential groupings of species with affinities for similar environmental conditions. The overall configuration of the species distribution provides critical insights into the dimensionality of the ecological variation. In this context, the two axes of the plot correspond to the two latent variables, which represent the minimum number of unobserved environmental gradients needed to capture the main ecological structure of the community. The spatial arrangement and relative scatter of the species points within this two-dimensional space reveal the degree of ecological specialization and the distinctness of species' niches, illustrating how the community partitions

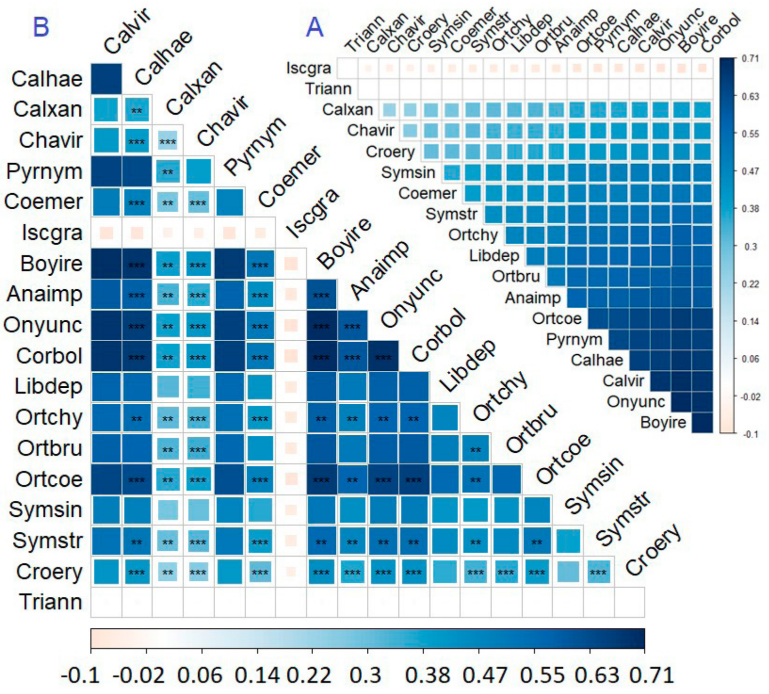

Figure 8. Correlation values from GLLVM models applied to a subset of the sampling data. A. Correlation values derived from a Negative Binomial GLLVM model applied to sampling locations of lotic habitats (Class I, 143 sites), considering the 19 species found within these locations. The conditions of the GLLVM model are the same as those described for figure 5A. B. Unordered correlation matrix for the data subset shown in panel A, developed using the visualisation options described in figure 5B ("original" option of corrplot). Significant correlations are indicated by asterisks based on bootstrap *p*-values (*** $p < 0.001$,** $p < 0.01$). Acronyms as in Table 2. *Valores de correlación de los modelos GLLVM aplicados a un subconjunto de los datos de muestreo. A. Valores de correlación derivados de un modelo GLLVM binomial negativo aplicado a los lugares de muestreo de hábitats lóticos (Clase I, 143 sitios), considerando las 19 especies encontradas dentro de estos lugares. Las condiciones del modelo GLLVM son las mismas que las descritas para la figura 5A. B. Matriz de correlación sin ordenar para el subconjunto de datos mostrado en el panel A, desarrollado utilizando las opciones de visualización descritas en la figura 5B (opción "original" de corrplot). Las correlaciones significativas se indican con asteriscos basados en los valores* p *del bootstrap (**** $p < 0.001$, ** $p < 0.01$)*. Acrónimos como en la Tabla 2.*

the available ecological space and how species respond to these major gradients.

Species assemblages in lotic habitats

In the headwaters of watercourses, extensive reaches spanning several kilometers and encompassing altitudinal gradients exceeding 500 meters commonly host *C. boltonii* as the sole odonate species. This community scheme is also evident along a gradient, when an analysis of the class I localities is performed for these same environmental variables (Fig. 8). We documented the presence of *C. boltonii* at high altitudes, reaching 2060 meters, where it was collected under a substantial ice layer. Its distribution spans a range of over 1700 meters. Below the *C. boltonii* dominance zone, a typical rheophilic assemblage of mountain zones includes *C. boltonii* alongside *C. virgo*, *C. haemorrhoidalis*, *B. irene*, *O. uncatus*, and *C. mercuriale*. In mid-altitude riverine zones, *C. xanthostoma* joins this community. With decreasing altitude, the community is successively joined by *P. nymphula*, *O. brunneum*, *O. coerulescens*, and *O. chrysostigma*. A specific odonate association constituted by *I. graellsii*, *A. imperator*, *C. erythraea*, and *S. fonscolombii* has been repeatedly observed in lower reaches of lotic habitats characterised by a high organic load.

Species assemblages in lentic habitats

The odonate community composition varies across these different habitat classes. In the lentic habitats (Classes II-IV) of the study area, a clear association exists among five

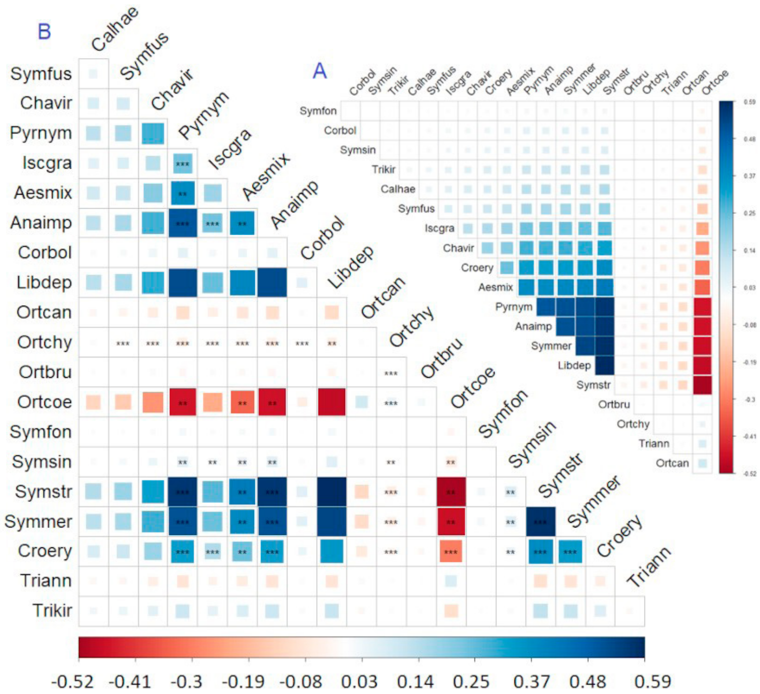

Figure 9. GLLVM results showing species correlations in a lentic habitat data subset. A. A Negative Binomial GLLVM model was applied to the 73 sampling locations designated as lentic habitats (Class II-IV) and the 20 species found there. Panel A displays the resulting correlation values; the model's conditions replicate those in figure 5A. B. Panel B provides the unordered correlation matrix for this subset, visualised using the "original" option of corrplot, consistent with figure 5B. Significant correlations, determined by bootstrap *p*-values, are denoted by asterisks (*** $p < 0.001$, ** $p < 0.01$). Acronyms as in Table 2. *Resultados del GLLVM que muestran las correlaciones de especies en un subconjunto de datos de hábitat léntico. A. Se aplicó un modelo GLLVM binomial negativo a los 73 lugares de muestreo designados como hábitats lénticos (Clase II-IV) y las 20 especies encontradas allí. El panel A muestra los valores de correlación resultantes; las condiciones del modelo replican las de la figura 5A. B. El panel B proporciona la matriz de correlación sin ordenar para este subconjunto, visualizada utilizando la opción "original" de corrplot, consistente con la figura 5B. Las correlaciones significativas, determinadas por los valores* p *del bootstrap, se denotan con asteriscos (*** $p < 0.001$, ** $p < 0.01$). Acrónimos como en la Tabla 2.*

species: *S. striolatum*, *S. meridionale*, *L. depressa*, *P. nymphula*, and *A. imperator*, with looser associations noted for *A. mixta* and *C. erythraea* (Fig. 9). High-altitude Class II aquatic ecosystems host a common odonate community. The core species are *P. nymphula*, *L. depressa*, *S. meridionale*, and *S. striolatum*. However, the overall community structure and species richness in these habitats vary, with up to nine species present, depending on the degree of naturalness and habitat stability. The full species list for Class II habitats also includes *C. viridis*, *L. barbarus*, *S. fusca*, *I. graellsii*, *E. cyathigerum*, *A. mixta*, *A. imperator*, *C. boltonii*, *O. chrysostigma*, *O. cancellatum*, *O. brunneum*, *C. erythraea*, and other species of *Sympetrum* (*S. fonscolombii* and *S. sinaiticum*). Class III habitats are characterised by a shift in family representation, where Lestidae species disappear, Coenagrionidae diversity decreases, and Libellulidae species become more prevalent. This is accompanied by the introduction of a higher proportion of generalist and opportunistic species in mid- and low-altitude zones, such as *O. chrysostigma*, *S. sinaiticum*, *C. erythraea*, *I. graellsii*, and *T. kirbyi*. Class IV associations, found above 1400 m, consist of water bodies formed from snowmelt, surface runoff, and springs. These habitats are defined by a core community of *L. depressa* accompanied by several *Orthetrum* species.

DISCUSSION

This study reveals distinct odonate community associations across different altitudinal zones and habitat types within the Sierra Nevada area. The majority of the species reported here are characteristic for both lotic and lentic habitats (such as *P. nymphula*, *C. xanthostoma, A. mixta*, *S. sinaiticum*), although predominantly lotic (such as *C. boltonii*, *B. irene*, *O. uncatus* and the three species of *Calopteryx*) and lentic species (such as *L. barbarus*, *S. fusca* and *Sympetrum* spp.) were also recorded (Table S1, supplementary information, available at https://www.limnetica.com/en/limnetica). Odonate presence in lotic habitats is influenced by several important parameters such as aquatic and riparian vegetation, water velocity, temperature, and substrate grain size. Furthermore, previous research (Hardersen, 2008, Silva et al., 2010, Golfieri et al. 2016) has shown that descriptors of polluted aquatic environments, such as chemical oxygen demand and total organic carbon play a significant role (likely from domestic sewage and other human activities). Based on the results from the analysis of class I localities, we can identify a distinct *Cordulegaster boltonii* Dominance Zone (CBDZ). This zone reflects the broad altitudinal tolerance of the species, which is distributed across a range of over 1700 meters. Its presence at 2060 meters, where it was collected under a substantial ice layer, represents one of the highest altitudinal limits within its peninsular distribution. Similarly, we can distinguish the Basic Rheophilic Association (BRA), the most frequent community found in the Sierra Nevada. This association, with significant ecological value, develops in fluvial reaches free from pollution and with well-developed riparian vegetation. The constituent anisopterans serve as biological indicators of the environmental health of watercourses, the functionality of their structure, and the good conservation status of the riparian forest. This underscores the importance of using these insect groups to assess the ecological integrity of riverine systems. In lotic headwaters, the dominance of *C. boltonii* (CBDZ) underscores its remarkable altitudinal tolerance, extending to some of the highest recorded limits for peninsular Iberian odonates. This contrasts with the more diverse Basic Rheophilic Association (BRA) found at lower altitudes, characterised by a consistent group of rheophilic species including *Calopteryx* spp., *B. irene*, and *O. uncatus*, alongside *C. boltonii*. The BRA's association with unpolluted fluvial reaches and well-developed riparian vegetation highlights the role of these odonates as indicators of stream health and habitat integrity, echoing findings in other Mediterranean mountain ranges (Jarry & Vidal, 1960, Ferreras-Romero, 1984, Martín & Maynou, 2016). The subsequent incorporation of species of genera *Orthetrum* and occasionally other species at even lower altitudes suggests a gradual shift in community composition driven by factors likely related to temperature and flow regime. Notably, the recurrent association of *I. graellsii*, *A. imperator*, *C. erythraea*, and *S. fonscolombii* in organically enriched lower reaches signifies the adaptation of specific odonate assemblages to altered water quality, with a broad biogeographic distribution (Chelli & Moulaï, 2019). The overarching pattern of odonate community structure in lotic systems appears to be influenced by water temperature (Bonacina et al., 2023).

Based on our findings, the Basic Lentic Association (BLA) is the most frequently observed odonate community in the high-altitude class II habitats of Sierra Nevada. This association is defined by the presence of its two key species, *S. striolatum* and *S. meridionale*, which are often accompanied by *L. depressa*, *P. nymphula*, and *A. imperator*. The presence of these two key species serves as a strong indicator of a developing and diverse community (Kolar et al., 2021, Minot et al., 2021). As these habitats mature and stabilize, additional species are gradually incorporated, but the core BLA structure remains centred on these foundational species. We have confirmed the presence of the BLA at altitudes up to 2560 m, which may represent the upper altitudinal limit for the Iberian distribution of this group. The variability in the BLA's species composition suggests that habitat naturalness and stability are crucial factors influencing the richness and structure of these communities. While a more diverse community of up to nine species can be found across the altitudinal gradient of class II habitats, the full range of odonate diversity found in other natural high-altitude ponds is sparsely represented within our specific sampling area. This limited representation warrants further investigation. Additionally, these diverse communities are notably vulnerable to anthropogenic pressures, such as livestock grazing, which can lead to habitat degradation and eutrophication. The change in odonate family representation in class III habitats—a decrease in Lestidae and Coenagrionidae and an increase in Libellulidae—alongside the presence of generalist and opportunistic species like *O. chrysostigma*, *S. sinaiticum*, *C. erythraea*, *I. graellsii*, and *T. kirbyi* at lower elevations, indicates the influence of habitat type and disturbance. The *Anax-Crocothemis* association, frequently observed in these artificial environments (García-Avilés et al., 1995), exhibits a broad geographic distribution, encompassing continental Europe (Carchini et al., 2007), several Mediterranean and Macaronesian islands, and North Africa (Ait Taleb et al., 2024). This likely represents an early stage of the *Ischnura* spp. association, a consequence of the temporary or structurally simple nature of these human-created habitats. The ecological significance of these secondary habitats for species like *T. kirbyi* and *S. sinaiticum*, of African origin that recently migrated to the Iberian Peninsula (Ferreras-Romero, 1989b, Cano-Villegas, & Conesa-Garcia, 2009), and various *Orthetrum* species, particularly in the more arid parts of the study area, highlights their potential role in regional odonate conservation. The presence of vagrant, migratory, or pioneer species in the mountain habitats of classes II and III emphasises the dynamic nature of these communities. The infrequent occurrence of associations above 2000 m in the Iberian context, with some representing potential glacial relics, underscores the conservation value of these high-altitude ecosystems (Martín, 2000, Flechoso et al., 2020, Sánchez Sastre, et al., 2020, Morales et al., 2022, Gómez-Vadillo et al., 2025). In the face of climate change, the observed species richness in these sensitive habitats and the potential colonisation of lower altitudes by new species serve as critical indicators for future monitoring efforts (Oertli, 2008, 2010, Lamouille-Hébert et al., 2024, 2025). Finally, the distinct associations of class IV water bodies, dominated by *L. depressa* and *Orthetrum* spp. at higher altitudes, further illustrate the influence of habitat origin and environmental conditions on odonate community composition in spring and seepage environments (Sánchez et al., 2009), subject to pronounced seasonality and extreme drying conditions (Piersanti et al., 2007, Rebora et al., 2007). The gray-blue generalist species *L. depressa* and *Orthetrum* sp., recognised for their pioneer nature (Boudot & Kalkman, 2015), exemplify the link between body coloration and thermal adaptation in odonates, a trait generally associated with body size (Acquah-Lamptey et al., 2020). Their northward expansion from the Ponto-Mediterranean area into the warmer regions of central Europe further supports this, as shown by Šigutová et al. (2025).

According to Buffagni (2021), the Lentic-Lotic River Descriptor (LRD) (Buffagni et al., 2010) serves as a valuable tool for quantifying these habitat preferences. Our findings align with this framework, showing distinct preferences among different odonate families. Specifically, the Lestidae family is associated with more lentic zones (10 ≥ LRD < 30). In contrast, Aeshnidae, Coenagrionidae (in part), and Libellulidae exhibit a stronger affinity for extremely lentic habitats (LRD ≥ 50). Therefore, the distribution of species should not be viewed as a rigid presence-absence pattern, but rather as a range of tolerance around an optimal point for each species. The diversity patterns observed, such as the shift in family prevalence from lotic to lentic environments, reflect these specific habitat preferences along the lotic-lentic gradient. For example, the decline of lotic-adapted species and the rise of lentic-adapted ones in class III habitats corresponds to a change in the LRD value, moving toward more standing-water conditions. This conceptual model provides a robust ecological basis for understanding the variations in community composition across the study area. The observed patterns in odonate community diversity can be effectively explained by considering the lotic-lentic character of their habitats. This is consistent with the established understanding that aquatic macroinvertebrate communities are strongly influenced by the flow regime of the watercourse.

Odonate conservation frequently needs a differentiated approach for Zygoptera (damselflies) and Anisoptera (dragonflies) due to their contrasting adult and larval ecologies. However, it is crucial to acknowledge that the larval stage also presents distinct conservation considerations for each suborder. For instance, habitat degradation can exert differential impacts on damselfly and dragonfly larvae, reflecting their divergent ecological niches and life history traits (Ferreras-Romero et al., 2009). The loss of emergent vegetation along lentic water body margins can severely compromise the larval survival and successful emergence of zygopteran species, such as those within the family Coenagrionidae, which frequently utilise these structures as emergence substrates. Conversely, the siltation of lotic riverbeds can be particularly detrimental to burrowing anisopteran larvae, exemplified by species like *O. uncatus*, which rely on interstitial spaces within the substrate for development and refuge. Moreover, the disparate larval prey requirements and foraging strategies characteristic of zygopteran and anisopteran larvae imply that alterations in invertebrate communities can elicit divergent effects on their development, growth rates, and overall survival. Understanding these distinct larval vulnerabilities is paramount for the implementation of effective and targeted conservation strategies for both damselflies and dragonflies across their entire life cycle. While adult ecological differences often dictate separate conservation strategies for damselflies and dragonflies, the challenges faced during their larval development are equally important to consider for effective odonate conservation. These challenges are often species-specific and can be quite distinct between the two suborders. Take, for example, the overwintering strategies: some damselfly larvae, like certain *Lestes* spp., undergo a diapause in the egg stage, avoiding harsh winter aquatic conditions, a strategy rarely seen in European dragonfly larvae. Similar to the challenges faced by high-mountain dragonfly larvae such as *Somatochlora alpestris*, which are adapted to survive in cold, high-altitude waters with short growing seasons (Billqvist et al., 2024), *C. boltonii* in Sierra Nevada is also affected by snow and meltwater runoff originating from elevations exceeding 3000 m, impacting its high-altitude habitat and presenting comparable cold-related challenges. Coping with such short, cold periods needs specific life history strategies, prominently including prolonged development cycles. For instance, *S. alpestris* exhibits a lengthy larval development period of typically 3 to 4 years in semi-permanent ponds. These extended life cycles and associated adaptations contrast sharply with those of many insect species inhabiting warmer, more stable environments, where development is often completed much more rapidly. The ecological significance of these secondary habitats in Sierra Nevada for odonate conservation is substantial. They are used by opportunistic species of African origin like *T. kirbyi* and *S. sinaiticum*, as well as several *Orthetrum* species (*O. chrysostigma*, *O. coerulescens*, and *O. brunneum*). These groups form an assemblage that is most prominent in the most arid sector of the study area.

This study establishes a valuable baseline for understanding odonate distribution patterns and community structure across the altitudinal gradients of Sierra Nevada. Through detailed characterisation of species occurrences and associations, we forged a critical ecological foundation. Our results, particularly the identification of distinct species groups and the correlation of their distribution with environmental parameters, provide a strong empirical basis for focused investigations into underlying ecological mechanisms. The observed community structure suggests the presence of unmeasured environmental drivers, forming a solid hypothesis that subsequent research must address by identifying specific factors such as microhabitat characteristics, water quality variables (e.g., oxygen levels, pH), riparian vegetation, and anthropogenic habitat alterations. Moreover, these baseline patterns are crucial for long-term ecological monitoring in Sierra Nevada, a high-altitude mountain range highly vulnerable to climate change. This foundation is vital for assessing the impact of rising temperatures on odonate altitudinal ranges, detecting upward shifts or local extinctions, and ultimately evaluating the effectiveness of existing conservation strategies to develop new, targeted plans for protecting these sensitive insect communities.

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AVAILABILITY STATEMENT

All data and R code used within this manuscript are available upon reader's request.

AUTHOR CONTRIBUTIONS

A.R.M.: Conceptualisation, Methodology; J.D.G.: Methodology; A.J.L.M.: Statistics; F. J.M.: Methodology, Statistics, Visualisation.

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